

EARLY PLIOCENE TETRAPOD REMAINS FROM KANAPOI, LAKE TURKANA BASIN, KENYA

JOHN M. HARRIS,¹ MEAVE G. LEAKEY,² AND THURE E. CERLING³

APPENDIX BY ALISA J. WINKLER⁴

ABSTRACT. Kanapoi, located in the southwestern portion of the Lake Turkana Basin, is the type locality of the oldest East African australopithecine species, *Australopithecus anamensis*, and has yielded a diverse tetrapod assemblage that includes more than 50 species. The terrestrial fossils derive from fluvial sands that date between 4.17 and 4.07 Ma and which sandwich a lacustrine interval that represents the extensive Lonyumun Lake—a predecessor of Lake Turkana. The tetrapod assemblage is broadly similar to comparably aged assemblages from the nearby locality of Lothagam and the slightly older site of Aramis in Ethiopia. Soil horizons from the succession suggest a mixture of habitats similar to those in the vicinity of the Omo Delta at the north end of the modern Lake Turkana. The Kanapoi biota, however, appears to represent a mixture of open and closed xeric habitats.

INTRODUCTION

The early Pliocene locality of Kanapoi is located to the southwest of Lake Turkana in northern Kenya at 36°3'51.1"E, 2°18'32.2"N. The Kanapoi sites were first collected in the mid-1960s (1965–67) by expeditions from Harvard University under the leadership of Bryan Patterson. Significant among the 400 specimens collected by the Harvard University parties are the holotypes of the elephantid *Loxodonta adaurora* Maglio, 1970, and rhinocerotid *Ceratotherium praecox* Hooijer and Patterson, 1972, two of the most characteristic components of the East African Pliocene biota, together with a hominid humerus that was tentatively identified as *Australopithecus* sp. (Patterson et al., 1970). Some elements of the fauna were described in detail, including proboscideans (Maglio, 1970, 1973), suids (Cooke and Ewer, 1972), and rhinos (Hooijer and Patterson, 1972), but the remainder of the material was largely overlooked.

Kanapoi was subsequently recollected in the mid-1990s by National Museums of Kenya expeditions under the leadership of Meave Leakey. The vertebrate fauna was considerably augmented and the hominid hypodigm was expanded to include cranial, dental, and postcranial material of *Australopithecus anamensis* Leakey et al., 1995, currently the oldest recognized East African australopithecine

(Ward et al., 2001). The age of the Kanapoi biota is tightly constrained to between 4.17 and 4.07 Ma (Leakey et al., 1998) and, as such, it documents a perilacustrine assemblage from an interval of time that is not well represented elsewhere in the Lake Turkana Basin.

We provide here a description of much of the fossil vertebrate material recovered by the Harvard University and National Museums of Kenya expeditions. The fish and carnivorans are described separately by Kathy Stewart and Lars Werdelin, respectively, in adjacent parts of this *Contributions in Science* issue, as is an assessment of the geologic context by Craig Feibel. The micromammals will be investigated by Frederick Kyalo of the National Museums of Kenya for his Ph.D. dissertation, but a preliminary assessment of this material by Alisa Winkler is appended to this contribution.

GEOLOGIC SETTING

The stratigraphic sequence at Kanapoi reflects deposition in fluvial and lacustrine environments and has been studied by Denis Powers (1980) and Craig Feibel (2003b). A basal fluvial complex of channel sandstones and floodplain paleosols lies on the dissected surface of Miocene volcanic rocks. Two devitrified tuffs in this lower fluvial unit have yielded dates of 4.17 ± 0.03 Ma (lower pumiceous tuff) and 4.12 ± 0.02 Ma (upper pumiceous tuff) (Leakey et al., 1995). In this unit, vertebrate fossils occur primarily in the vertic floodplain paleosols. The basal complex is overlain by claystones with ostracods and mollusks; these were deposited within the early Pliocene Lonyumun Lake that extended throughout much of the Lake Turkana Basin. The vitric Kanapoi Tuff from the upper portion of the lower lacustrine sequence con-

1. George C. Page Museum, 5801 Wilshire Boulevard, Los Angeles, California 90036, USA.

2. National Museums of Kenya, PO Box 40658, Nairobi, Kenya.

3. Departments of Biology and Geology & Geophysics, University of Utah, Salt Lake City, Utah 84112, USA.

4. Shuler Museum of Paleontology, Southern Methodist University, Dallas, Texas 75275, USA.

tained pumices that were dated to 4.07 ± 0.02 Ma (Leakey et al., 1998). This tuff cannot be matched with any tephra exposed in the northern part of the Lake Turkana Basin but shows affinity with tephra from the Lake Baringo Basin. The lacustrine strata are overlain by extensive deltaic sandstones that are rich in vertebrate remains, and these are in turn overlain by a second fluvial interval that has extensive conglomeratic channels near its top. The sequence is capped by the Kalokwanya Basalt that has been dated to 3.4 Ma, providing an upper limit on the age of the formation (Feibel, 2003b).

CONVENTIONS AND ABBREVIATIONS

The full accession number for Kanapoi specimens housed at the National Museums of Kenya in Nairobi begins with the prefix KNM-KP (e.g., KNM-KP 435). This prefix is abbreviated to KP in the descriptive portions of the text and omitted altogether in the list of Kanapoi material at the beginning of each systematic section. The following abbreviations appear in the lists of specimens and in the tables:

ant	=	anterior
ap	=	anteroposterior
BL	=	buccolingual
dist	=	distal
EK	=	Ekora
frag	=	fragment
h/c	=	horn core
juv	=	juvenile
KP	=	Kanapoi
LL	=	labiolingual
LT	=	Lothagam
Lt	=	left
lt	=	length
MD	=	mesiodistal
mand	=	mandible
max	=	maxilla
met	=	width at metaloph(id)
m/p	=	metapodial
m/t	=	metatarsal
PL	=	plastron length
post	=	posterior
prot	=	width at protoloph(id)
prox	=	proximal
p/c	=	postcranial
Rt	=	right
tr	=	transverse

SYSTEMATIC DESCRIPTION

Order Chelonia

Family Pelomedusidae

Turkanemys Wood, 2003

Turkanemys pattersoni Wood, 2003

KANAPOI MATERIAL. 435, carapace; 436, carapace; 437, carapace frags; 451, carapace frags; 562, partial carapace and plastron; 30174, cara-

pace and plastron; 30438, carapace and plastron; 30470, carapace and plastron; 30595, carapace; 30597, carapace and plastron; 30618, carapace and plastron.

Turkanemys pattersoni was recently described from Lothagam (Wood, 2003). Its shell differs from all other African pelomedusid species by virtue of having trapezoidally shaped first vertebral scute and in the tendency of the nuchal bone to be proportionally broader than in other species. The shell differs from all South American species of *Podocnemis* (to which many African fossil pelomedusids have been referred in the past as a matter of convenience) in having six rather than seven neural bones and a triangular rather than pentagonal intergular with gulars meeting in the midline behind it. *Turkanemys pattersoni* also differs from all other pelomedusid species in the structure of the cervical series, with articular surfaces being intermediate in shape between saddle joints of typical podocnemines and procoelous condition of pelomedusines and *Erymnochelys madagascariensis* Grandier, 1867. *Turkanemys pattersoni* is the most common chelonian from Kanapoi.

Kenymys Wood, 1983

Kenymys sp. indet.

KANAPOI MATERIAL. 30419, carapace frags; 30468, juvenile carapace and plastron.

Kenymys williamsi Wood, 1983, differs from all other known pelomedusids by the following combination of characters: (a) a series of elongate tuberosities forming an interrupted keel extending along the midline rearward from the dorsal surface of the second neural bone; (b) six neural bones forming a continuous series, the anterior end of the first abutting directly against the rear margin of the nuchal bone and the sixth one being heptagonal; (c) outer corners of nuchal bone extending beyond lateral margins of first vertebral scute; (d) pentagonal shape of first vertebral scute; (e) only eighth and posterior part of seventh pair of pleural bones meet at midline of carapace; (f) anterior plastral lobe truncated; (g) triangular intergular scute not overlapping anterior end of entoplastron and only partially separating the gular scutes along the midline axis of the plastron (Wood, 1983). The occurrence of two pelomedusid specimens with a midline keel on the carapace indicates the presence of an as yet undetermined species of *Kenymys*.

Family Trionychidae

Tribe Cyclanorbini

Cyclanorbis Grey, 1854

Cyclanorbis turkanensis Meylan et al., 1990

KANAPOI MATERIAL. 17196, carapace missing the eight pair of costals and the lateral portions of all the left costals (holotype).

Only one specimen (the holotype) of this taxon

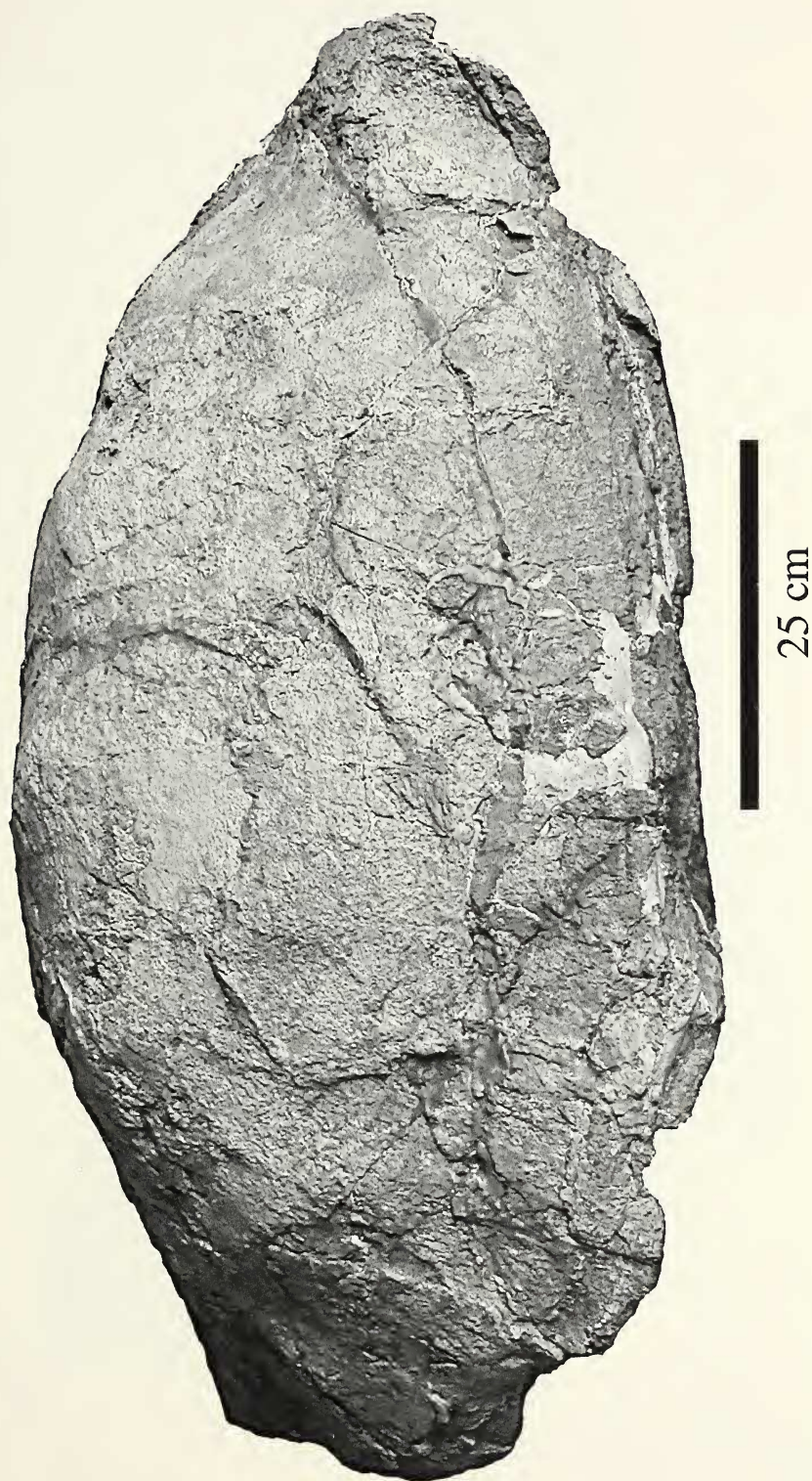


Figure 1 KNM-KP 10552; *Geochelone crassa* shell, dorsolateral view; scale = 25 cm

is known from Kanapoi. The distinctly concave lateral margins of the carapace posterior to the fourth costal together with the hypertrophied and distinctly V-shaped cross-section of the vertebrae centra distinguish this species from other species of *Cyclonorbis*.

Cyclanorbini gen. and sp. indet.

KANAPOI MATERIAL. 17202, carapace.

A relatively complete cyclanorbin carapace unfortunately lacks the diagnostic scutes that would permit identification beyond the tribal level.

Trionychidae gen. and sp. indet.

KANAPOI MATERIAL. 30605, carapace and plastron frags.

This specimen comprises fragments of carapace and plastron of a single individual that have the sculpted morphology characteristic of trionychid turtles but which cannot be identified beyond the family level.

Family Testudinidae

Geochelone Fitzinger, 1835

Geochelone crassa Andrews, 1914

(Figure 1)

KANAPOI MATERIAL. 10552, complete shell; 30199, carapace and plastron.

Geochelone is an almost cosmopolitan tortoise genus in which the carapace and plastron are never hinged and which often achieved large size. *Geochelone crassa* is a large (>700 mm PL) African form in which the pectorals are widest at the midline but narrow considerably on either side of the midline; gulars and pectorals fall short of the entoplastron. This species is based on a partial plastron from the early Miocene locality of Karungu (Meylan and Auffenberg, 1986:281) but evidently survived into the Pliocene. Meylan and Auffenberg (1986) identified KP 10552—a nearly complete but crushed, meter-long shell of a large land tortoise—as *G. crassa* (Fig. 1) but erroneously documented the accession number as 10052. They noted that most of the shell was badly broken but sulci and bone sutures are visible on the ventral surface of the anterior lobe of the plastron. The pectorals are widest at the midline (110 mm) but narrow laterally (to 30 mm). The gular scutes appear to reach the entoplastron but the pectorals do not.

cf. *Geochelone* sp. indet.

KANAPOI MATERIAL. 30439, carapace and plastron; 30614, half carapace and plastron.

Several specimens comparable in size to, or smaller than, the extant leopard tortoise *Geochelone pardalis* Bell, 1828 were recovered from Kanapoi by National Museums of Kenya expeditions.

Order Crocodylia

Family Crocodylidae

Crocodylus Laurenti, 1768

Crocodylus niloticus Laurenti, 1768

(Figure 2)

KANAPOI MATERIAL. 18333, Lt. mand frag; 18334, Lt. mand frag; 18336, incomplete skull; 18337, young skull; 18338, adult skull; 30196, articulated skull and mand; 30437, skull frags; 30492, cranial frags, scutes, and p/c frags; 30594, partial skull and mandible; 30604, skull.

The extant Nile crocodile is a moderate- to large-sized crocodylid with generalized rostrum of moderate proportion, median nasal promontorium, typically 14 maxillary and 15 mandibular teeth and with the anterior nuchal osteoderms well developed (Storrs, 2003). Ten relatively complete *Crocodylus niloticus* crania and/or mandibles were collected by National Museums of Kenya expeditions (Fig. 2). Tchernov (1976, 1986) had reported that the broad-snouted *Rimasuchus lloydi* (Fourteau, 1920) was the common crocodilian in the Lake Turkana Basin and that *C. niloticus* had a very sparse record in the Plio-Pleistocene. However, Storrs (2003) documented the presence of five crocodilian taxa, including both *R. lloydi* and *C. niloticus* at Lothagam. Even so, it was somewhat surprising to find ten *C. niloticus* cranial specimens in the Kanapoi biota but only one of *R. lloydi*. Nevertheless, the apparent dominance of the extant Nile crocodile in the Kanapoi biota must be viewed with caution because only the more complete crocodilian specimens were collected.

?*Crocodylus* sp. indet.

(Figure 3)

KANAPOI MATERIAL. 30451, rostrum and symphysis frags.

Associated rostrum and symphysis fragments document the presence of a second species of broad-nosed crocodile. This species can be distinguished from broad-nosed crocodilians previously documented from the Pliocene of East Africa by its unusually long mandibular symphysis. *R. lloydi* and the extant species *C. niloticus* and *C. cataphractus* Cuvier, 1824, all have short mandibular symphyses whereas that of KP 30451 is more than 10 cm long. This undetermined species is also characterized by the broad and straight anterior margin of the snout. No other fossil or extant crocodilian species is known to possess this combination of features (G. Storrs, personal communication).

Rimasuchus Storrs, 2003

Rimasuchus lloydi (Fourteau, 1920)

(Figure 4)

KANAPOI MATERIAL. 30619, anterior rostrum and mandible frags.



Figure 2 KNM-KP 18338; *Crocodylus niloticus* cranium, dorsal view; scale = 5 cm

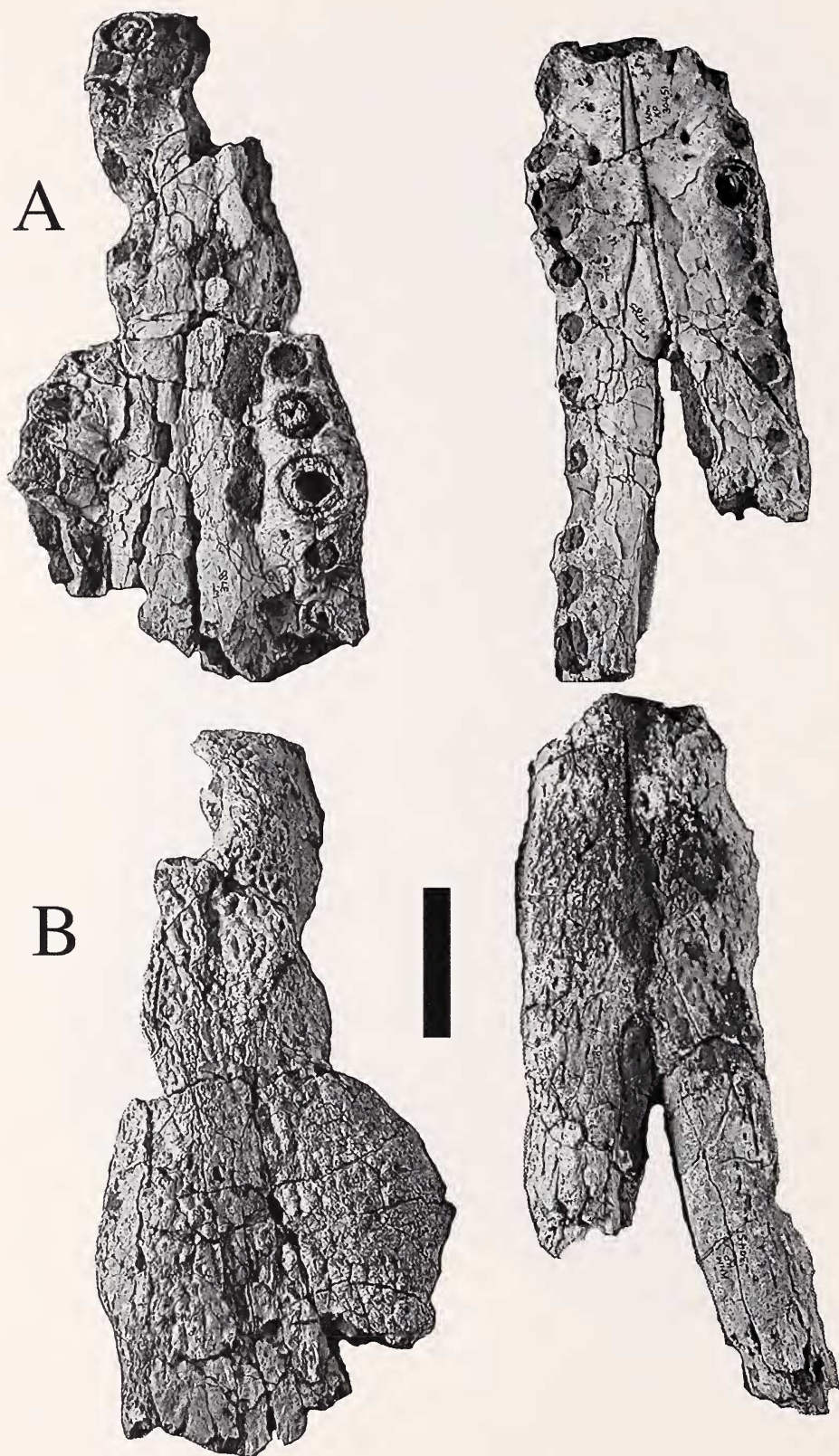


Figure 3 KNM-KP 30451; ?*Crocodylus* sp., cranium and mandible fragments; A = occlusal views of anterior rostrum and mandibular symphysis; B = dorsal view of anterior rostrum, ventral view of mandibular symphysis; scale = 5 cm

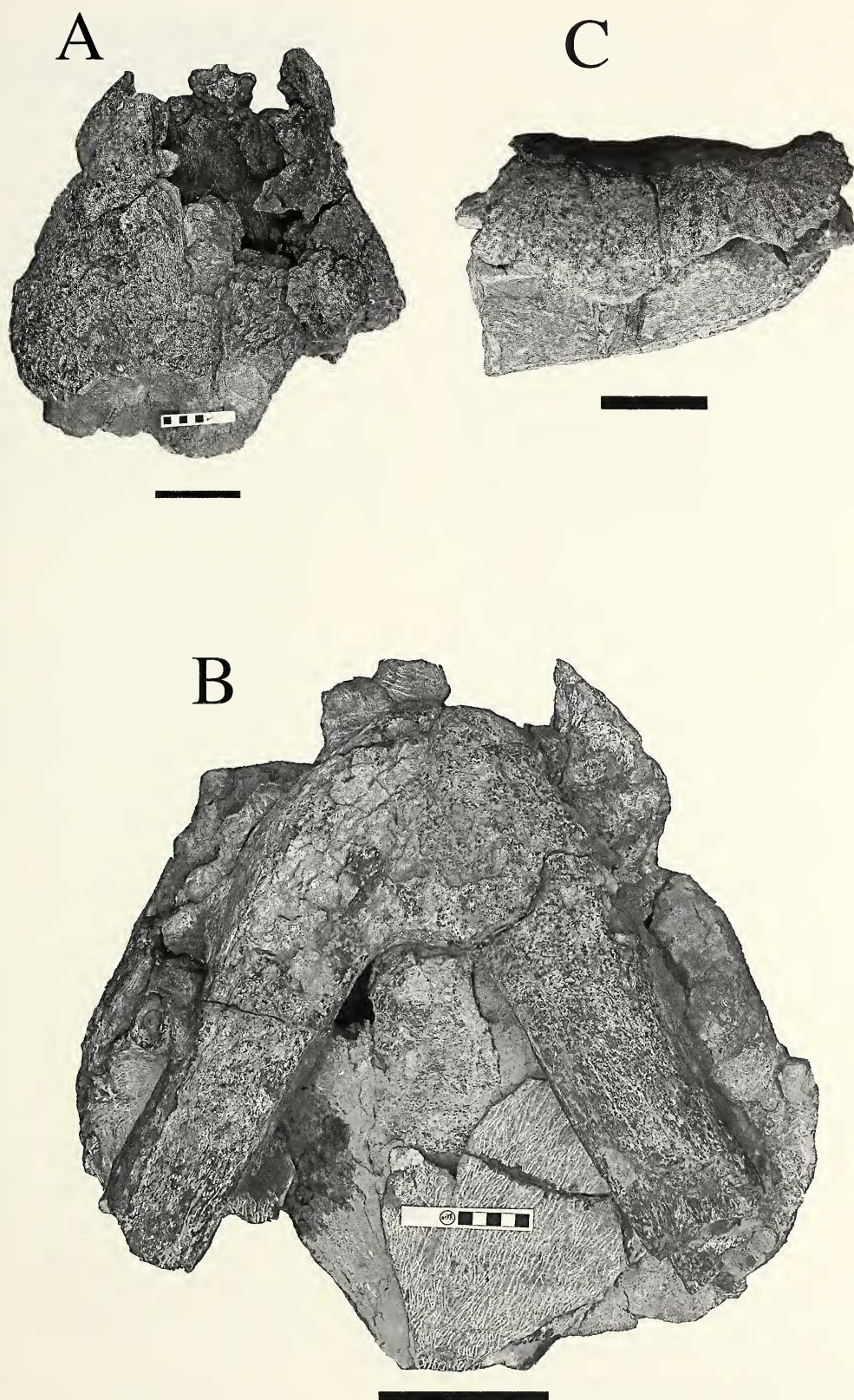


Figure 4 KNM-KP 30619; *Rimasuchus lloydi*, anterior rostrum and mandible fragments, A = dorsal view; B = ventral view; C = lateral view; scales = 10 cm

The genus *Rimasuchus* was proposed by Storrs (2003) for a very large, brevirostrine crocodylid that had been previously referred to *C. lloydi*. The species is characterized by premaxillae that are broader than long and that had a relatively straight premaxillae/maxillae palatal suture, a deep "canine" occlusal notch, a slight dorsal maxillary boss, closely spaced anterior dentary teeth, broadly diverging mandibular rami, and prominent dentary festoons. It is readily distinguished from *C. niloticus* by the lack of a nasal promontorium.

An anterior portion of a very large rostrum with associated mandible was recovered from just below the Kanapoi Tuff. Measuring 326 mm across the widest preserved portion of the anterior rostrum, the specimen represents the largest crocodylian individual yet recovered from the Lake Turkana Basin. The most distinctive features of *R. lloydi*, other than the absence of a nasal promontorium, are its relatively short but broad premaxillae and its short and deep mandibular symphysis. The conformation of the Kanapoi specimen leaves no doubt that it represents *R. lloydi*.

Euthecodon Fourtau, 1920

Euthecodon brumpti (Joleaud, 1920)

KANAPOI MATERIAL. 18330, complete skull and mand; 18331, rostrum frag; 18332, articulated skull and mand frag; 30653, mand symphysis; 30176, edentulous mand; 30266, mand frags; 30407, mand.

Euthecodon brumpti is a very large eusuchian in which the extremely elongate and narrow rostrum has deeply scalloped dental margins. The premaxillae and nasals are attenuated but the narial ridge is prominent. A moderate premaxillary/maxillary diastema is located behind four premaxillary teeth. The skull table is small and nearly square, the occiput vertical, the mandibular symphysis long, and the teeth isodont and slender (Storrs, 2003).

Half a dozen specimens of slender-snouted crocodilians were recovered by National Museums of Kenya expeditions. These clearly belong to *E. brumpti*, a species distinguished by its slender snout and long slender curved teeth, rather than to the gavial reported by Storrs (2003) from the lower Nawata Formation at the nearby site of Lothagam.

Order Struthioniformes

Family Struthionidae

Struthio Linnaeus

Struthio sp. indet.

KANAPOI MATERIAL. 29300, eggshell frags; 30221, eggshell frags; 30223, eggshell frags; 30262, eggshell frags; 30490, eggshell frags; 32522, eggshell frags; 36599, eggshell frags.

Several occurrences of fossil ostrich eggshell fragments were noted on the surface of the fossiliferous strata at Kanapoi and several voucher specimens

were collected by National Museums of Kenya expeditions. These shell fragments all had the struthious pore pattern characteristic of living ostriches (Sauer, 1972) and the pore basins are of similar size and shape to those reported from the upper Nawata at Lothagam (Harris and Leakey, 2003a). The $\delta^{13}\text{C}$ content of the fossil eggshell is more negative than those of extant ostriches from Kanapoi and the $\delta^{18}\text{O}$ is more positive. It would appear that there was a greater proportion of C_3 vegetation in the Pliocene ostrich diet compared with that of modern ostriches on the west side of Lake Turkana.

Order Pelecaniformes

Family Anhingidae

Anhinga Brisson, 1760

Anhinga sp. indet.

KANAPOI MATERIAL. 39325, Lt. humerus.

This family is represented by the left humerus of a darter of comparable size to the extant African darter.

Order Ciconiiformes

Family Ciconiidae

Mycteria Linnaeus

Mycteria sp. indet.

KANAPOI MATERIAL. 30231, Lt. dist tibia, prox Rt. tibiotarsus, Lt. radiale, and long bone frags.

Storks were represented at Kanapoi by a single association of long bone fragments.

Order Charadriiformes

Family Anatidae

Gen. and sp. indet.

KANAPOI MATERIAL. 39326, proximal Lt. humerus.

The Anatidae was represented at Kanapoi by a goose-sized left humerus fragment.

Order Primates

Family Galagidae

Galago Geoffroy, 1796

The modern species range in size from the largest *Galago crassicaudatus* Geoffroy, 1812 (1,122–1,750 g) to the smallest, *Galago demidovii* (Fisher, 1806) (69–81 g), and they inhabit a variety of habitats including primary and secondary lowland and montane forests, gallery forests, *Acacia* woodlands, savannahs, thorn scrub, and forest edge.

cf. *Galago* sp. indet.

(Figure 5)

KANAPOI MATERIAL. 30260 Rt. mand frag. (M_2).

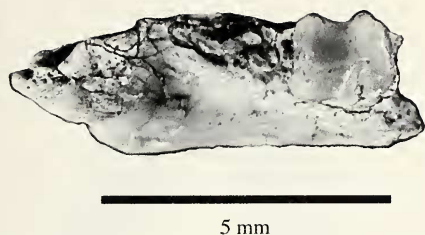


Figure 5 KNM-KP 30260; cf. *Galago* sp. indet., right mandible fragment (M_2), occlusal view; scale = 5 mm

Mandibular fragment, KP 30260, is approximately the size of *Galago demidovii*, the smallest living galago. The specimen is too fragmentary to allow precise identification. Due to their small size, galagos are rare in the fossil record and little is known of their distribution or evolution in the Pliocene.

Family Cercopithecidae

Subfamily Colobinae

Although rare elements in fossil assemblages, the Colobinae were a diverse group in the Pliocene, at which time they appear to have undergone a major radiation. Several species of large colobines are known from Pliocene and early Pleistocene deposits in the Turkana Basin, the Baringo Basin, and from Olduvai (Leakey, 1982, 1987). The postcranial morphology indicates differing degrees of arboreality but all appear to have been more terrestrial than extant east African colobines. Fossil Colobinae include at least three genera—*Paracolobus* Leakey, 1969, *Rhinocolobus* Leakey, 1982, and *Cercopithecoides* Mollet, 1947—and are known from several relatively complete skeletons. Smaller colobines were also diverse but are less well represented by fossils. The genus *Kuseracolobus* Frost, 2001 has been described from early Pliocene deposits at Aramis in the Awash Valley, Ethiopia, where colobines constitute an unusually high proportion (56%) of the cercopithecoid assemblage. At Kanapoi, at least three species are represented, two moderately large but of indeterminate affinities, and the other an indeterminate species of *Cercopithecoides*. Such diversity at Kanapoi indicates that the colobine radiation began prior to 4.1 million years ago.

Cercopithecoides Mollet, 1947

Cercopithecoides is one of the best-represented colobine genera in the East African Pliocene and early Pleistocene. Until recently, only two East African species were recognized, *C. williamsi* Mollet, 1947, and *C. kimeui* Leakey M. G., 1982, but additional taxa are now described from Lothagam (Leakey et al., 2003) and at Leadu in Ethiopia (Frost and Delson, 2002). Features of the postcranial anatomy in-

dicate that *Cercopithecoides* was probably the most terrestrial of the Pliocene colobines.

cf. *Cercopithecoides* sp. indet.
(Figure 6; Tables 1, 2, 4)

KANAPOI MATERIAL. 29255, mandible (Rt. P_3 – M_3 , Lt. P_3 – M_1); 31741, broken M^1 or M^2 ; 32870, Lt. P_4 ; 36967, Lt. M^3 ; 37382, Rt. $/C$; 43120, P_3 talonid.

A handful of specimens represent a small species of colobine. The well-preserved mandible permits tentative taxonomic assignment to *Cercopithecoides*. The mandible probably represents a female: although the canines are lost, their alveoli are not large and the honing facet of the P_3 is short. The symphysis is broken toward the alveolar margin, the right body extends behind the M_3 , and the left body terminates behind M_1 . The M_1 s are quite heavily worn, the M_2 and the premolars less so, and the M_3 has relatively light wear. Slight damage to the body beneath the P_3 s on both sides may well be from carnivore chewing.

The mandibular morphology is similar to that of *Cercopithecoides* with a relatively shallow and moderately thick mandibular corpus. However, the anterior face of the symphysis lacks a median mental foramen and is more sloping and less flattened than in other known species. Below the deep genio-glossal pit, the inferior torus is well developed. Although the canines are missing and the alveoli damaged, the dental arcade appears to be narrower between the canine alveoli. The inferior margin of the mandibular body is clearly defined anteriorly where there is a distinct and deep digastric fossa that merges posteriorly with the submandibular fossa. The mylohyoid line is prominent, providing considerable strength to the body and defining the upper extent of the submandibular fossa. With the exception of the less worn M_3 , the teeth are heavily worn, as is so often the case with *Cercopithecoides*.

Colobinae gen. et sp. indet. A
(Figure 7; Tables 1–3)

KANAPOI MATERIAL. 31736, skull frag and male associated lower teeth (I, and Lt. P_4 , partial Lt. and Rt. C, Rt. P_3 , and molar, and molar frag); 29307, Rt. juv mand (dP_4 , I_1 – P_4 in crypts); 30408, Lt. mand (erupting P_3 and P_4 , M_{1-2}); 30496, Lt. $/C$; 32803, Rt. M_{1or2} ; 32525 male partial Lt. C; 32821, Lt. M_2 ; 36830, Lt. mandible (M_1 , crypt for M_2).

The specimens assigned to this taxon are fragmentary, largely subadult, and mostly from the lower jaw. They represent a fairly large colobine that has relatively large high-crowned premolars (compared with the size of the molars). The unerupted P_3 of KP 30408 has a large protoconid and distinct metaconid as well as a large distal fovea. The remaining specimens are tentatively referred to this taxon but could equally well belong to the following taxon.

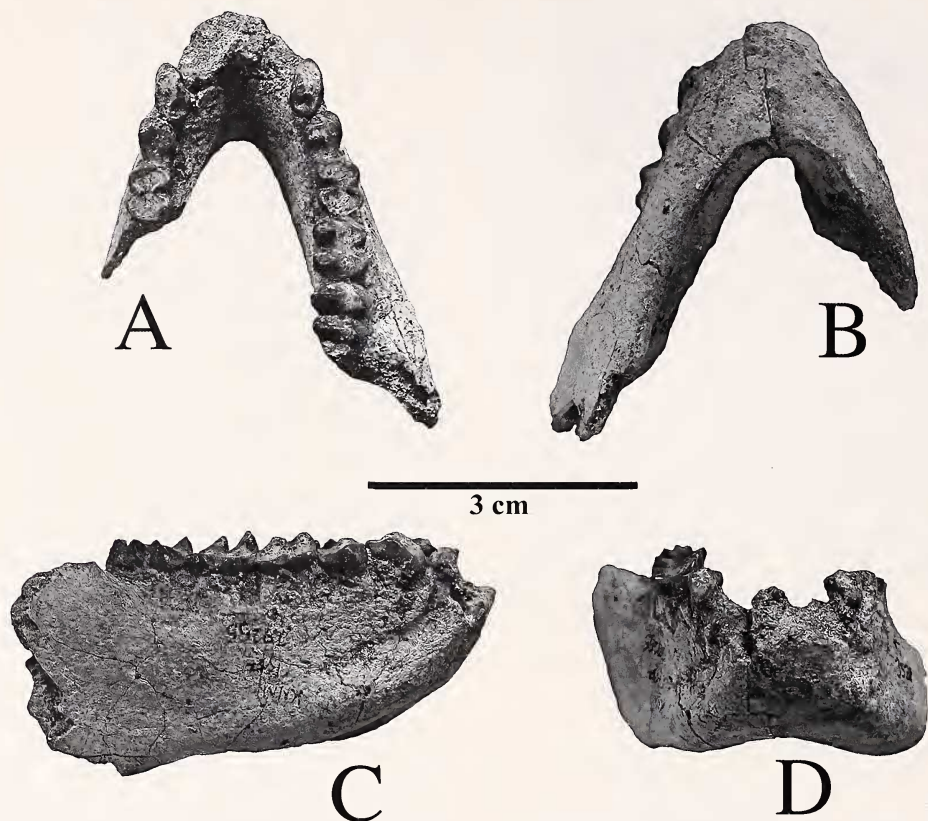


Figure 6 KNM-KP 29255; cf. *Cercopithecoides* sp. indet., mandible (Lt. P₃–M₁, Rt. P₃–M₃), A = occlusal view; B = inferior view; C = right lateral view; D = anterior view; scale = 3 cm

Colobinae gen. et sp. indet. B
(Figure 8; Table 2)

KANAPOI MATERIAL. 29308, male Lt. mand (erupting P₃, roots C, P₄–M₁).
This is a juvenile mandible with the P₃ erupting. Although of similar size, the P₃ differs significantly from that of Colobinae gen. et sp. indet. A. It has a large single cusp, the protoconid, and a small distal fovea in contrast with the two cusps and large distal fovea of KP 30408.

Table 1 Kanapoi Colobinae upper dentition measurements

	M ³	
	MD	LL
cf. <i>Cercopithecoides</i> sp. indet.		
36967	8	8.2
	C/	
Colobinae gen. et sp. indet. A	MD	LL
32525	7.3	12.9

Subfamily Cercopithecinae
Tribe Papionini

The Papionini are the dominant cercopithecids in most Pliocene and Pleistocene sites in East Africa. *Parapapio* Jones, 1937, was the common genus in the early Pliocene, but was later replaced by *Theropithecus* Geoffroy, 1843. At Aramis, in the Middle Awash, a new 4.4 million year old papionin, *Pliopapio alemui* Frost, 2001, has been recovered (Frost, 2001). *Pliopapio* Frost, 2001, is distinguished from *Parapapio* by the presence of an anteorbital drop, a distinct ophryonic groove, and a shorter and more rounded symphyseal profile. The absence of an anteorbital drop is the sole diagnostic character separating *Parapapio* from *Papio* Müller, 1773.

Genus *Parapapio* Jones, 1937

Parapapio is recorded from almost all East African Pliocene sites, and is generally believed to have given rise to *Papio*, from which it can be differentiated only by its facial profile. A number of species have been described and differ largely on the basis of size—a criterion that is not easy to apply when

Table 3 Kanapoi Colobinae gen. et sp. indet. A deciduous teeth

Lower dentition	dP ₄	
	MD	BL
29307	6.6	4.7

there is some degree of sexual dimorphism. *Parapapio* was the most common cercopithecoid in the South African Pliocene and early Pleistocene sites where *P. jonesi* Broom, 1940, *P. broomi* Jones, 1937, and *P. whitei* Broom, 1940, are recognized. In East Africa, *Parapapio* is less well known but, prior to the appearance of *Theropithecus*, is the dominant cercopithecoid at most Pliocene sites in the Turkana Basin (e.g., Allia Bay, Kanapoi, and Lomekwi). *Parapapio ado* (Hopwood, 1936) is recognized at Laetoli, Tanzania (Leakey and Delson, 1987) and *Parapapio* cf. *P. jonesi* at Hadar (Frost and Delson, 2002).

Parapapio ado (Hopwood, 1936)
(Figure 9; Tables 5–8)

KANAPOI MATERIAL. 286, male mandibular symphysis (roots Lt. and Rt. I₁–C), Lt. mandibular frags (P₄–M₁), (M₃), Rt. mandibular frag (M_{2–3}); 26942, Rt. mand (M_{1–3}); 29295, Rt. M₂; 29304, Lt. mand frag (worn M_{1–2}, M₃ talonid); 29305, Rt. M₃; 29306, male Lt. mand (P₃–M₃, root /C, alveoli Lt. and Rt. I₁–I₂); 29310, Rt. M₂; 29312, Lt. mand frag (M_{2–3}), Lt. P₄, mand and tooth frags; 30147, male edentulous mandibular symphysis (roots Lt. and Rt. C, P₃, alveoli Lt. and Rt. I_{1–2}), frags Lt. mandible (roots M_{1–3}); 30148, Rt. female C/; 30149, juvenile mand (Lt. d/C, dP_{3–4}, M₁, Rt. dI₂–M₁), Lt. juvenile max (dC/, dP_{3–4}, M₁, C/ in crypt), Rt. juvenile max (dP₃–M₁) isolated Lt. and Rt. dI₁, I₁, Rt. dC/, skull frags; 30213, Rt. M₂; 30230, female Rt. mand (P₃–M₃), Lt. mand (M_{1–3}), isolated Lt. and Rt. I₁, I₂ and Lt. P₃; 30233, Lt. male mand (M₃, roots /C–M₂), Rt. mand frag (root /C); 30398, worn and broken Rt. M₂ and mand frag; 30399, Rt. M₃; 30434, Rt. dI₁; 30483, Lt. M₃; 30531, squashed anterior female mand (broken Lt. and Rt. I₁–P₄); 30532, Lt. mandible (broken P₄–M₂); 30535, Rt. M₃; 29311, Lt. I₂; 30538, female max, mand, and skull frags; Rt. mandible (broken and

Table 4 cf. *Cercopithecoides* sp. indet mandibular measurements

	29255
Depth below P ₄ /M ₁ junction	20.9
Depth below M ₂ /M ₃ junction	21.4
Max thickness below M ₁	10.4
Max thickness below M ₃	10.9
Length tooth row P ₃ –M ₃	39.8



2 cm

Figure 7 KNM-KP 30408; Colobinae gen. et sp. indet. A, left mandible, occlusal view; scale = 2 cm



2 cm

Figure 8 KNM-KP 293080; Colobinae gen. et sp. indet. B, left mandible, occlusal view; scale = 2 cm

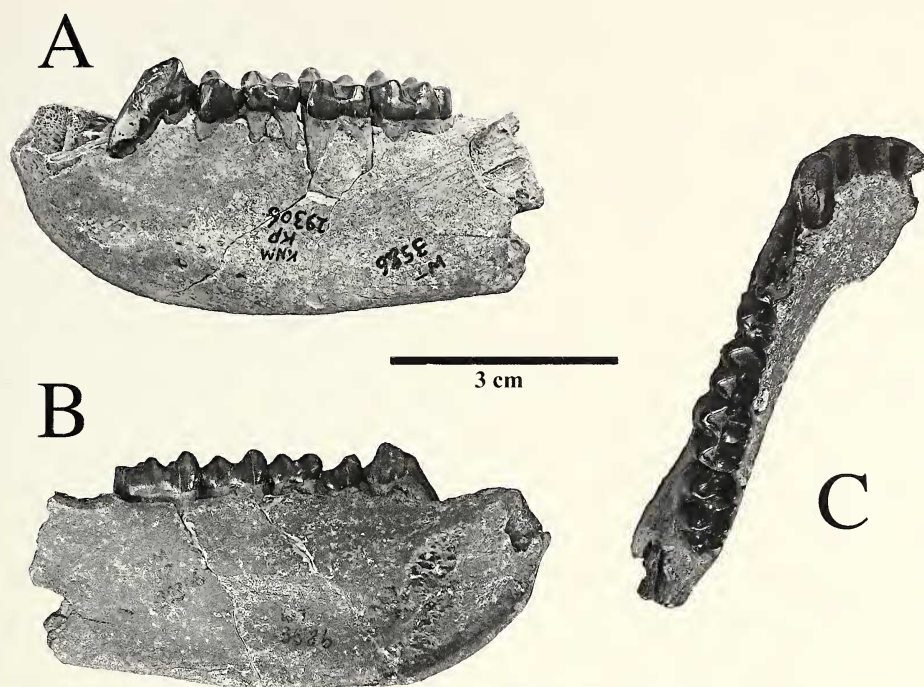


Figure 9 KNM-KP 29306; *Parapapio ado*, left male mandible (P_3 – M_3), A = lateral view; B = medial view; C = occlusal view; scale = 3 cm

cracked I_1 – M_3), Lt. mandible (I_2 – M_1), Lt. I_1 , M_3 , / M ; Lt. maxilla (I^1 – P^3) broken Rt. C/, broken Lt. P^4 , M^1 , M^2 , M^3 ; 30539, Rt. M_3 ; 32512, Lt. M^3 ; 32520, female edentulous mand (roots Lt. I_1 – M_1 and Rt. I_1), Rt. I_2 ; 32527, Lt. dP^4 ; 32534, Rt. M^1 or M^2 ; 32535, Rt. M_2 ; 32554, Rt. male C/; 32572, Lt. dP_4 ; 32804, mesial frag Lt. M_3 ; 32805, partial Rt. M^1 ; 32806, Rt. M_3 ; 32811, broken Rt. M_2 ; 32816, Rt. I_1 ; 32817, worn Rt. M_3 ; 32819, Rt. max (P^3 – P^4), frag edentulous Lt. premax; 32869, Rt. M_3 , and Lt. /C; 32878, Rt. dP^3 ; 32884, Lt. d/C; 36914, Lt. M_2 , partial / M ; 36969, Rt. female /C, M frag, Lt. P^4 ; 37374, tooth frags—molar and premolar upper and lower, dist phalanx; 37378, broken M , tooth frag; 37379, Lt. /I, talonid Lt. M_3 ; 37380, broken Lt. I_2 ; 43121, Rt. female /C; 43122 dP_4 .

The Kanapoi *Parapapio* material is rather fragmentary and consists mainly of isolated teeth. Two mandibular specimens are well preserved in addition to the mandible KP 286 that was recovered by the earlier expeditions and initially attributed to *Parapapio jonesi* (Patterson, 1968). KP 29306, a male left mandibular body, includes the entire symphysis extending to the right canine alveolus. The symphyseal morphology is close to that of KP 286, although it is shallower and in profile less steeply inclined with a slight curvature. The body is not deep and is quite slender with well-preserved P_3 – M_3 . KP 30147 is a mandibular symphysis that has suffered some postmortem expansion, making it appear larger than KP 286. If allowance is made

for the distortion, the symphyseal morphology is similar to the other two specimens. All three mandibles have a distinct mental foramen and may be distinguished from *Pliopapio alemui* by the steeply sloping symphysis and the angle of the incisor roots, which shows the incisors to have been procumbent rather than vertically set. Two specimens, KP 30149 and KP 30538, have well-preserved upper and lower juvenile dentitions.

The M_3 has an unusually large talonid and talonid basin, such that the hypoconulid is of almost equal size or in some cases (KP 30233) larger than the distal lingual cusp (entoconid). This feature, which occurs with a relatively high frequency at Kanapoi but is unusual in other species of *Parapapio*, may possibly be of taxonomic significance.

Theropithecus Geoffroy, 1843

Theropithecus first appears in the Turkana Basin about 3.5 million years ago, although one older tooth from Allia Bay may possibly represent this genus and a partial tooth from Kanapoi is here assigned to *Theropithecus*. At Pliocene localities younger than 3.5 million years, *T. brumpti* (Arambourg, 1947) became the dominant cercopithecoid until it was replaced by *T. oswaldi* (Andrews, 1916) at about 2.5 million years (Leakey, 1993).

cf. *Theropithecus* sp. indet.

KANAPOI MATERIAL. 32879, broken Rt. M_{1or2} .

Table 5 Kanapoi *Parapapio ado* upper teeth measurements

	Side	I ¹		I ²		C/		P ³		P ⁴		M ¹		M ²		M ³		
		MD	LL	MD	LL	MD	LL	Height	MD	BL	MD	LL	MD	BL	MD	BL	MD	LL
29310																		
29311				4.2	5.3												9.6	9.3
30148	Female	R				6.8	6.8	10.9										
30149		L	7.5	6.0	~4.8	4.4						9.3	8.1					
30149		R	7.5	~5.8								9.3	8.0					
30538	Female	L	6.5	6.1	>3.9	4.9			6.7	5.0	5.7	7.0	8.2		9.8		9.5	9.5
30538		R					>6.3											
32512		L					>5.9	5.6									10.6	10.1
32534															>10	8.6		
32805															8.3	>6.8		
32819		R							>5.3	7.1	5.3	7.4						
32554		R					11.6	8.8										
36969		L									5.6	7.4						

This tooth is larger than any of the *Parapapio* first and second molars (MD length 11.6; BL distal breadth 8.0). It is incomplete, lacking most of the lateromesial cusp both mesial and lateral to the preserved cusp tip. The deep valleys and high cusps indicate affinities with *Theropithecus*. As such, this is one of the earliest occurrences of this genus.

Cercopithecidae gen. et sp. indet.
(Figure 10)

KANAPOI MATERIAL. 458, prox Lt. ulna, dist femur; 29292, partial Lt. femur shaft; 29303, dist Rt. humerus; 29309, Lt. astragalus; 30424, prox Rt. femur; 30431, prox Rt. radius; 30460, prox Lt. femur; 30529, prox Rt. femur; 32516, Lt. C/; 32562, phalanges, phalanx shaft, prox m/p, patella, rib frags; 32818, frags of calcaneum, femur head, long bone frags; 32880, caudal vertebra; 36601, proximal phalanx; 36831, prox Lt. ulna frag; 36834, distal Rt. humerus; 36837, Rt. astragalus.

A complete, slender, high-crowned canine (KP 32516) represents a small monkey. Crown measurements are MD length, 3.9; LL width, 6.3; max crown height, 13.0. The height of the crown suggests it must be from a male. The size is too small for it to belong to the Kanapoi *Parapapio*. It may possibly be referable to cf. *Cercopithecoides* sp. indet., the small colobine described above, but the slender nature of the canine is unlike other colobines. For now it is left as *Cercopithecidea* gen. et sp. indet.

Two fragments of distal humerus are morphologically similar but very different in size. The medio-lateral width of the smaller, KP 29303, is 22.5 mm, in contrast with the larger KP 36834, which measures 30.4 mm. Both are reasonably well preserved although, on both, there is some weathering of the medial epicondyle and along the lateral edge of the capitulum. The trochlear flange is relatively lightly developed and the olecranon fossa elongated lateromedially, quite deep but not perforated. Compared with the *Parapapio lothagamensis* humeri described from Lothagam (Leakey et al., 2003), the medial epicondyle is less posteriorly directed, the trochlear flange less strongly developed, and the olecranon fossa more elongated lateromedially without any proximal extension to accommodate the ulna olecranon process in extension. The distal humerus of *Cercopithecoides* is closer in all these characters to those from Lothagam than to the two specimens from Kanapoi.

Two partial ulnae were recovered, KP 458 and KP 36831. The former is well preserved, small, lightly built, and most probably colobine. Its short olecranon process is slightly deflected posteromedially. The radial notch appears to show some indication of a double articular facet. KP 36831 is slightly larger, less well preserved, and squashed, but is morphologically similar to KP 458.

The shaft of the proximal radius, KP 30431, extends 30 mm below the radial tuberosity. The ar-

Table 7 *Parapapio ado* deciduous teeth

	Side	dI ¹		dI ²		dC/ Height			dP ³		dP ⁴	
		MD	LL	MD	LL	MD	LL		MD	BL	MD	BL
Upper dentition												
30149	L	6.0	3.6			5.2	3.7		7.5	6.0	8.5	6.9
30149	R	6.1	3.4			5.2	3.6		6.8	6	8.5	6.9
30434	R	5.8	3.6									
32572	L										7.3	6
32878	R								7	6.3		
	Side	dI ₁		dI ₂		d/C			dP ₃		dP ₄	
		MD	LL	MD	LL	MD	LL	Height	MD	BL	MD	BL
Lower dentition												
30149	L			4	2.8	3.5	4.2	>5.2	6.8	4.5	7.1	5.9
30149	R					3.6	4.3		6.9	4.4	7	6
32527	L										6.8	5.5
32884	L					2.9	4.3					
43122											6.5	5.2

ticular surface of the head is almost circular, with a distinct depression for articulation with the humerus capitulum. It is tilted with the posteriomedial edge higher than the opposite side; the anterolateral portion of the collar surrounding this depression is widest. The head measures 15.5 mediolaterally by 14.5 anteroposteriorly. The radial tuberosity is well developed with a raised and rounded anterior border and a less prominent crest marking the posterior margin. The interosseous crest commences about 10 mm below the most distal extent of the radial tuberosity.

Three fragments of proximal femora, KP 30460, 30424, and 30529, and a proximal femur shaft, KP 29292, have been recovered. 30460 has lost the margins of the greater tuberosity, 30424 lacks the head, and 30529 has lost both the greater and lesser tuberosities. KP 458 is a distal epiphysis with approximately 25 mm of shaft. The neck of KP 30424 is relatively long compared with those of the Lothagam femora, and the articular surface of the slightly larger head projects onto the femoral neck. The greater tuberosity of KP 30460 is relatively large and would have extended proximal to the head. KP 30529 is significantly smaller than the other fragments. The proximal shaft KP 29292 has

a pronounced crest on the posterior face proximal to the commencement of the linea aspera.

Two complete tali were recovered. The maximum length of the smaller, KP 29309, is 23 mm; that of the larger, KP 36837, is 27 mm. KP 29309 has a carnivore tooth mark on its trochlear surface. Both specimens have relatively long necks.

The affinities of the postcranial elements are unclear. In general, they appear to be from similar sized individuals, but the size discrepancy between the two morphologically similar distal humeri suggests these elements may represent one sexually dimorphic species.

DISCUSSION

Sites close in age to Kanapoi that have yielded early cercopithecids include Aramis (4.4 Ma), Allia Bay (3.9 Ma), Laetoli (3.6 Ma), and the Sidi Hakoma (3.4–3.22 Ma), Denen Dora (3.22–3.18 Ma), and lower Kada Hadar (3.18–2.92 Ma) members of the Hadar Formation in the Awash Valley. Aramis is unusual in having a larger proportion of colobines to cercopithecines (56% colobines). Only two cercopithecoid species are recognized from Aramis—*Kuseracolobus aramisi* Frost, 2001, and *Pliopapio alemui*. Neither is represented at Kanapoi. The Allia Bay cercopithecids are largely represented by isolated teeth that are difficult to assign taxonomically. However, papionins far outnumber colobines. At Laetoli, the common cercopithecoid is *Parapapio ado*, although cf. *Paracolobus* sp. is also relatively common. Unfortunately there are no well preserved P₃s in the Laetoli assemblage that can be compared with the two differing large colobine P₃s from Kanapoi. It is possible that one of the Kanapoi colobines is the Laetoli species. Present but uncommon at Laetoli was a small indeterminate co-

Table 8 Kanapoi *Parapapio ado* mandibular measurements

	29306
Depth below P ₄ /M ₁ junction	27.1
Depth below M ₂ /M ₃ junction	24.7
Max thickness below M ₁	9
Max thickness below M ₃	9.3
Length tooth row P ₃ –M ₃	35.4

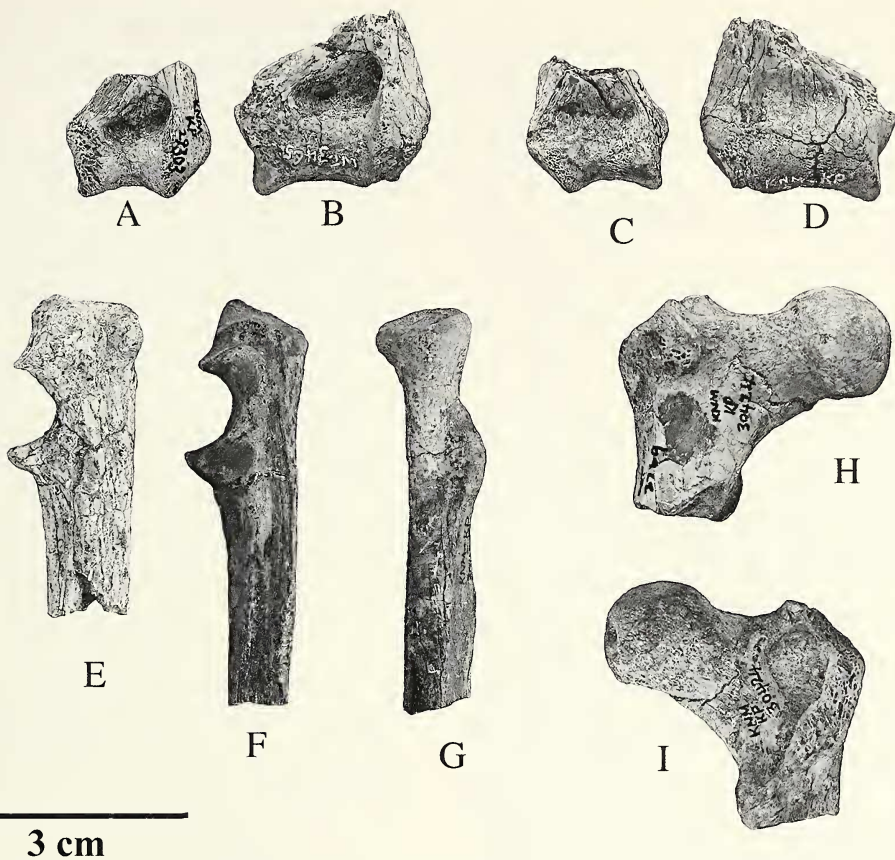


Figure 10 Cercopithecidae gen. et sp. indet., postcranial elements; distal right humerus: A, C = KNM-KP 29303, B, D = KNM-KP 36834; A, B = posterior view, C, D = anterior view; E = KNM-KP 458, proximal left ulna, F = KNM-KP 36831, proximal left ulna; G = KNM-KP 30431, proximal right radius, E, F, G = lateral view; H, I = KNM-KP 30424, proximal right femur, H = anterior view, I = posterior view

lobine and a large papionin cf. *Papio* sp. (Leakey and Delson, 1987). The cercopithecids from Hadar include *Theropithecus darti* (Broom and Jenson, 1946) and *Parapapio* cf. *P. jonesi*, as well as the colobines *Rhinocolobus turkanaensis* Leakey M.

G., 1982, and a new species of *Cercopithecoides* (Frost and Delson, 2002).

Family Hominidae

Australopithecus Dart, 1925

Australopithecus anamensis Leakey et al., 1995

Table 9 Kanapoi *Deinotherium bozasi* tooth measurements

Accession No.		401	30152
Lt. M ²	ap	92.1	
	prot	92.4	
	met	90.8	
Lt. M ³	ap	96.5	
	prot	99.0	
	met	90.1	
Lt. M ₃	ap		87.5
	prot		79.9
	met		67.9

KANAPOI MATERIAL. 271, distal Lt. humerus; 29281, holotype mandible and Lt. temporal; 29282, Lt. M_{1/2}; 29283, maxilla; 29284, Rt. P₃ and Rt. /C germs; 29285, Rt. tibia lacking midshaft region; 29286, mandible fragments and associated lower teeth (Rt. I₁, Lt. and Rt. I₂-M₃); 29287, mandible with teeth; 30498, Lt. and Rt. maxilla fragments and associated dentition; 30500, mandibular fragments and associated dentition (Rt. I₂-P₄, M₂₋₃); 30502, Rt. M₃, partial Lt. /M, molar frags; 30503, proximal manual middle phalanx; 30505, broken molar germ; 30942, five molar frags; 31712, associated juvenile mandibular and dental fragments; 31713, Rt. mandible with tooth frag-

ments; 31714, Lt. dP₄; 31715, Lt. M_{1/2} and two associated tooth frags; 31716, P^{3/4} fragment and C/ frags; 31717, Lt. M³, Rt. M₃, and Lt. M₂ frags; 31718, Rt. mandible frag (M₂₋₃); 31719, I¹; 31720, maxillary M fragment; 31721, Rt. M² and M³ partial crowns; 31723, Rt. M³; 31724, Lt. capitate; 31726, Rt. P⁴; 31727, Rt. /C; 31728, Lt. M₁; 31729, Rt. dP₂; 31730, Lt. M₂, Rt. P₃; 31732, tooth frags; 34725, associated juvenile dentition and skull frags; 35838, Lt. M₃; 35839, Lt. I¹, Rt. C/, and Lt. P₃; 35840, Lt. M³ and upper tooth frags; 35841, M crown; 35842, Rt. M^{21 or 22}; 35844, M frag; 35845, M frag; 35847, Lt. M₂; 35850, M/ frag; 35851, Lt. M^{1/2} frag; 35852, Lt. C/; 37522, Lt. /M; 37523, M frag; 37524, tooth frags.

Australopithecus anamensis is distinguished from all other australopithecine species by the following features: a small external acoustic meatus presenting a narrow ellipse in outline; long axes of mandibular bodies and tooth rows nearly parallel and close together; mental region of mandible not strongly convex; long axis of symphysis slopes markedly posteroinferiorly; canines with very long robust roots, trigons of upper molars much wider than talons, distal humerus with thick cortex enclosing a small medullary cavity. It can be distinguished from *A. afarensis* Johanson et al., 1978, by the following: upper canine root and associated facial skeleton less posteriorly inclined; lower molars tend to have more sloping buccal sides and upper molars more sloping lingual sides; tympanic plate horizontal without defining grooves. It can be distinguished from *Ardipithecus* White et al., 1994, by the following features: absolutely and relatively thicker enamel; upper canine buccal enamel thickened apically; molars more buccolingually expanded; first and second molars not markedly different in size; tympanic tube extends only to the medial end of the postglenoid process, rather than to the lateral edge or beyond it; lateral trochlear ridge of humerus weak (Leakey et al., 1995).

Australopithecus anamensis is the oldest reliably dated *Australopithecus* species. It was a habitual biped and is readily distinguishable from *A. afarensis* to which it may have been ancestral. A detailed account of the Kanapoi material, and of slightly younger material of *A. anamensis* from Alia Bay, was provided by Ward et al. (2001).

Order Proboscidea

Family Deinotheriidae

Deinotheres are Neogene proboscideans that differed from gomphotheriids and elephantids by retaining only the lower tusk and by never developing horizontal tooth replacement for their low-crowned lophodont teeth. Adapted for browsing on forest vegetation, they were common elements of the early Miocene African assemblages but are encountered only in small numbers in Pliocene and Pleistocene assemblages.

Deinotherium Kaup, 1829

Deinotherium bozasi Arambourg, 1934 (Table 9)

KANAPOI MATERIAL. 388, enamel frags and postcranial elements; 393, atlas; 401, Lt. M² and M³; 30152, Lt. M₃; 30557, partial M.

Deinotherium bozasi was a large African deinotheres with teeth of similar size to the European species *Deinotherium giganteum* Kaup, 1829. The skull rostrum was steeply downturned anteriorly (like that of *Prodeinotherium hobleyi* [Andrews, 1911]) but the external nares and rostral trough were narrower than in *D. giganteum*. As in *P. hobleyi* but in contrast with *D. giganteum*, the preorbital swelling is reduced and situated just in front of P³, the occiput is steeply inclined, and the nasal bones have a slight anterior median projection (Harris, 1978).

Deinotheres are represented at Kanapoi by a couple of isolated teeth and, perhaps, by ribs and vertebrae of a juvenile proboscidean that were associated with unerupted deinotheres enamel fragments. The upper second and third molars are distinctly smaller than the equivalent teeth on the somewhat younger *D. bozasi* skull from Koobi Fora (Harris, 1976a) and the lower third molar is smaller than the equivalent tooth in early Pleistocene deinotheres.

Family Gomphotheriidae

Gomphotheriids were the common proboscideans in African Miocene assemblages but only *Anancus* lingered into the early Pliocene.

Anancus Aymard in Dhorlac, 1855

Anancus kenyensis (MacInnes, 1942) (Table 10)

KANAPOI MATERIAL. 384, Lt. M₂; 410, Lt. M₂, Lt. and Rt. M₃.

Anancus kenyensis has been diagnosed by Coppen et al. (1978) as "a progressive species of *Anancus* with four and one half to five or more cone pairs on M2 and five and one half or more on M3; the crown is complicated by the presence of enamel columns partially fused into the faces of the main cones."

Anancus kenyensis is the last gomphotheriid species to survive in sub-Saharan Africa. Three *Anancus* teeth were recovered from Kanapoi by the Patterson expeditions of 1965 and 1966. Tassy (2003) recognized two different populations of *A. kenyensis*—a primitive or *kenyensis* morph with tetralophodont second molars based on the holotype of *A. kenyensis*, from Kanam (MacInnes, 1942) and a derived or *A. k. petrocchi* morph with pentalophodont second molars based on the sample from Sahabi (Libya) described by Petrocchi (1954). The *A. kenyensis* morph was recognized in samples collected from Kanam, Lukeino, Mpesida, and

Table 10 Kanapoi *Anancus kenyensis* tooth measurements

Accession No.	384	410	410	410
Tooth	LM ₂	LM ₂	RM ₃	LM ₃
No. plates	5	5	6	
No. plates in wear	5	5	3	
Length	156.25	146.6	220	
Length wear surface			91.6	
Width (greatest)	75.89	68.64	81	79
Height (middle plate)	67.54		60.9	64.09
Enamel thickness			5.04	

Lothagam, whereas the *A. k. petrocchi* morph is represented at Sahabi (Libya) and at Aterir, and in the Chemeron Formation in the Baringo Basin, as well as at Lothagam. The second molars recovered from Kanapoi display the derived traits—accessory conules, fifth lophid, and strong anancoidy—that are characteristic of the *A. k. petrocchi* morph (Tassy, 2003).

Family Elephantidae

The Family Elephantidae originated in the late Miocene of Africa. *Stegotetrabelodon* Pettruchi, 1941, and *Primelephas* Maglio, 1970, are the dominant elephantids at Lothagam (Tassy, 2003). *Elephas ekorensis* Maglio, 1970, first appears in the Apak Member at Lothagam together with an early *Loxodonta* F. Cuvier, 1925, species. *Elephas ekorensis*, and *Loxodonta adaurora* appear to be the characteristic elephantids of the African early Pliocene.

Elephas Linnaeus

Elephas ekorensis Maglio, 1970

(Figure 11; Tables 11, 12)

KANAPOI MATERIAL. 382, Rt. P⁴ frag; 392, P₂; 395, M₃ frag; 400, mand (P₂); 409, Rt. and Lt. mand frags (M₂); 411, Lt. M₃ frag; 412, M₂; 452, Rt. P₃; 28442, Lt. and Rt. P₃ frags; 30189, Lt. M₃; 30197, skull (RP²⁻³, Lt. P²⁻³); 30236, M₃; 30404, Rt. and Lt. P³⁻⁴, skull frags; 30625, M₁ frag and unerupted M₂ frags; 30639, mand (Rt. M₂, Lt. M₁₋₂); 32575, Lt. mandible (P₃₋₄); 30198, Lt. mand (M₁₋₂); 387, RM₃; 26956, Rt. mand (M₁); 30169, Lt. juv mand (P₂₋₃); 30170, Lt. juv mand (P₃) and symphysis; 30173, Lt. mand frag (P₃), frags unerupted P₄; 30175, mand (Lt. P₃, dP₄, Rt. P₄); 30270, Lt. and Rt. P²⁻⁴ and tusk frag eaten by hyena; 30471, Lt. mand (M₂ and M₃) and symphysis; 38975, Rt. M₃.

Elephas ekorensis is an early species of *Elephas* that was diagnosed by Maglio (1973) as having molars with crown height 10–15% greater than width, M3 broad anteriorly, becoming very narrow posteriorly; greatest width at base of crown; enamel loops prominent; enamel only very weakly folded near the base, 3–4 mm thick. The enamel plates are

well separated with lamellar frequency of 3.8–4.8. The plate formulae are M3 11/12, M2 ?/?, M1 7/8 (Maglio, 1973).

Elephas ekorensis and *Loxodonta adaurora* are the two common proboscideans from Kanapoi. The teeth of *E. ekorensis* may be generally distinguished on the basis of their narrower width, greater number of plates, greater lamellar frequency, and thinner and more convoluted enamel (Fig. 11). Unworn tooth plates have more apical digitations than those of *Loxodonta* teeth. Mandibles of *E. ekorensis* are proportionately narrow; the ventral surface is horizontal but curves down in front of the symphysis to terminate in a beak, which curves abruptly anteroventrally and is smaller and more gracile than that of *L. adaurora*. The upper second premolar sometimes has two plates (KP 30197) but the lower has three (KP 30150). The third premolars have six plates and are wider posteriorly. The fourth premolar and first molar have eight plates.

Elephas ekorensis is one of the oldest recognized species of *Elephas*. It has been recovered from the Apak Member of the Nachukui Formation at Lothagam, where it is preceded in the Upper Nawata Member by *Elephas nawataensis* Tassy, 2003, which Tassy (2003) interprets as intermediate between the earlier *Primelephas gomphotheroides* Maglio, 1970, and *E. ekorensis*.

Loxodonta F. Cuvier, 1825

Loxodonta adaurora Maglio, 1970

(Figure 12; Tables 13, 14)

KANAPOI MATERIAL. 381, Lt. and Rt. mand (M₁); 383, Lt. and Rt. M₃; 383, Lt. M₃ and frags; 385, holotype mand and skeleton; 389, M₃ frags; 390, Rt. and Lt. M₃ frags; 391, M₁ frag and pc; 394, radius and ulna; 396, Rt. M₂; 403, mand (Lt. M₂₋₃), pelvis, and femur; 406, Rt. mand frags (M₁₋₂); 407, RM₃; 548, Lt. M₃ frags; 28441, M₂ frag; 30150, P₂; M_{2-or3} talonid; 30188, Rt. maxilla (worn M₃); 30191, max frag (Lt. M₃); 30193, Lt. and Rt. mand (M₃) and frags; 30204, skull (Rt. and Lt. M₃), damaged posteriorly; 30269, mand (Rt. and Lt. M₂₋₃); 30436, P₂; 30596, mand M₂₋₃ (needs preparation); 30616, mandible (Lt. and Rt.



Figure 11 KNM-KP 30175; *Elephas ekorensis* mandible with Lt. P₃, P₄, Rt. P₄, occlusal view; scale = 5 cm

P₃, P₄); 30654, Rt. M₃; 32542, mand (Rt. and Lt. M₂₋₃).

Loxodonta adaurora was diagnosed by Maglio (1970) as a *Loxodonta* species with low-crowned molars, height equal to or less than width; enamel not folded, 3–5 mm in thickness; very large anterior and posterior columns, partially fused into plates but free at their apices, forming prominent median loops with wear; plates thick and well separated, lamellar frequency from 2.6 to 4.4. The plate formulae: M3 8–10X/10–11x, M2 7–8x/6–8x, M1 7/6–7 dm4 5/5–6, dm3 5/5–6, dm2 3/3 (Maglio 1973).

The holotype of *Loxodonta adaurora*, a skull and partial skeleton, was collected from Kanapoi in 1965 and described by Maglio in 1970 but unfortunately was badly damaged during its subsequent transportation back to Kenya. Some less complete specimens were collected by National Museums of Kenya expeditions during the 1990s. In general, *L. adaurora* teeth may be distinguished from those of *E. ekorensis* because they are wider, have fewer plates, and have thicker and less convoluted enamel; unworn tooth plates have a posterior median pillar and fewer apical digitations. The horizontal ramus of the mandible tends to be bulbous because of the greater width of the *L.*

adaurora teeth. The ventral surface of the mandible curves downward anteriorly at the rear of the symphysis to terminate in a robust beak. The cusps of the second premolars tend to remain isolated rather than fused into transverse plates. Fourth premolars and first molars have seven plates.

Loxodonta exoptata (Dietrich, 1941)
(Figure 13)

Kanapoi Material. 30611, Rt. mandible (M₂).

Loxodonta exoptata was originally recognized from the 3.5 Ma Laetoli Beds of Laetoli in Tanzania (Beden 1987). The teeth are more hypsodont than those of *L. adaurora* and have more plates but thinner enamel. In early wear, the plates form a loxodont pattern strongly reminiscent of the extant *L. africana* (Blumenbach, 1797). Molar fragments attributed to *Loxodonta* aff. *L. exoptata* have been recovered from the Apak Member at Lothagam (Tassy, 2003).

A partial mandible with lower second molar from high in the succession is the sole representative of *Loxodonta exoptata* from Kanapoi. It has eight plates, each with a posterior median pillar,

Table 11 Kanapoi *Elephas ekorensis* upper teeth measurements

Accession No.	30197		30197	382	30197
Tooth	LP ²		RP ²	LP ³	LP ³
No. plates			5+		6
No. plates in wear			2		6
Length	24.75		23.57		68.7
Length wear surface			16.75		62.3
Width (widest plate)	23.12		21.29	40.24	
Height (middle plate)			37.74		
Enamel thickness			1.7		
Laminar frequency			9E		10
Accession No.	30197	30404	30404	30404	30404
Tooth	RP ³	LP ³	RP ³	LP ⁴	RP ⁴
No. plates	6	6	6	5+	5+
No. plates in wear	6	6	6	1	1
Length	70.54	60.4	62.11		
Length wear surface	57.76	59.45	59.33	8.42	9.59
Width (widest plate)	43.44	40.68	39.63	51.74	52.43
Height (middle plate)			42.58	42.67	
Enamel thickness	1.73	1.84	2.14		2.39
Laminar frequency	10	9	9	6	6
Accession No.	412	387	411	30189	
Tooth	LM ²	M ² ³	RM ³	LM ³	
No. plates	7+				
No. plates in wear	4				
Length					
Length wear surface	122.87				
Width (widest plate)	77.95	80.18E	77.69	85.42	
Height (middle plate)	99.05				
Enamel thickness	2.9	3.34	5.42	4.24	
Laminar frequency	5E4.5	4+	5.5	5	
Accession No.	EK 424	EK424			
Tooth	RM ³	LM ³			
No. plates	10+	12			
No. plates in wear	?	4			
Length	269+	280			
Length wear surface		128.11			
Width (widest plate)	91	95.46			
Height (middle plate)	112	120.06			
Enamel thickness		5.15			
Laminar frequency	5	5			

and thick enamel. The rear of tooth is wider than the front.

Order Perissodactyla

Family Rhinocerotidae

The extant genera *Ceratotherium* Gray, 1867, and *Diceros* Gray, 1821, first appear in the late Miocene but at Lothagam are accompanied by the teleoceratine rhino *Brachypotherium* Roger, 1904 (Harris and Leakey, 2003b). Thus far, only the extant genera have been recovered from Kanapoi.

Ceratotherium Gray, 1867

Ceratotherium praecox
Hooijer and Patterson, 1972
(Figure 14; Table 15)

KANAPOI MATERIAL. 30, Rt. nasal boss, occiput frag, and skull frags; 32, incomplete rami (Lt. and Rt. P₃–M₃); 33, Lt. mand frag (M₂); 36, skull (Lt. M²⁻³, Rt. P⁴–M³) holotype; 38, Rt. P⁴ frag, tooth frags; 538, dist Lt m/t III; 30187, partial skull (P³⁻⁴); 30195, Lt. humerus; 30217, Lt. mand (P₃); 30554, Lt. P₄; 32556, Lt. dP/ frag; 32868, Lt. P₄.

Table 12 Kanapoi *Elephas ekorensis* lower teeth measurements

Accession No.	400	30169	411	30169	30170	30173	30175	32575
Tooth	LP ₂	LP ₂	LP ₃	LP ₃	LP ₃	LP ₃	LP ₃	Lt. P ₃
No. plates	4	4	6	6	6	6	5+	5
No. plates in wear	none	2	6	1	none	6		5
Length	25.76	26.14	66.53+	68.1	62.66	70.33		
Length wear surface	none	11.58	66.53	5.53	none	62.69		
Width (widest plate)	19.59	18.79		40.51	42.46	41.86	39.74	24.
Height (middle plate)	15.21			30.05	32.26			
Enamel thickness		0.97	1.6		2.79	1.71	1.97	2.3
Laminal frequency	20E	20E	9E	9E	9E	9E	10E	13
Accession No.		28442	30175	30175	32575	409	26956	
Tooth	Lt P ₄	Lt P ₄	LP ₄	RP ₄	Lt. P ₄	LM ₁	RM ₁	
No. plates	8	8	9	9	8+	8	7+	
No. plates in wear	8	8	5	5	3	1	3	
Length	68.6	68.6	113.2	116.95	106E	167E	120.46+	
Length wear surface			62.58	72.84	25	24.07	54.1	
Width (widest plate)	36.7	36.7	50.6	53.43		59.99	57.7	
Height (middle plate)						71.03	76.1	
Enamel thickness	2		2.5	2.57	2.5	3.61	2.72	
Laminal frequency	8			8	9E	6.5	6	
Accession No.		30198	30639	30639	30198	30639		
Tooth	LM ₁	LM ₁	Rt. M ₁	LM ₂	Lt. M ₂			
No. plates			8		9x			
No. plates in wear	5+		8	3				
Length			135		179			
Length wear surface	96.13		61	54.19				
Width (widest plate)	63.51+							
Height (middle plate)					85			
Enamel thickness	3.41		3.56	4.13				
Laminal frequency	5E		6.5	5E	5			

Table 12 Continued

Accession No.	30236	30471	30625	38975
Tooth	Rt. M ₃	Lt. M ₃	Lt. M ₃	Rt. M ₃
No. plates	8+	13	6+	7+
No. plates in wear		3		4
Length	223+	276		
Length wear surface		75.79		
Width (widest plate)		86.47	75	80+
Height (middle plate)		105.7	95e	
Enamel thickness	100	5.05	4.5	4
Lamellar frequency	3.5	5	5	4.5

Ceratotherium praecox appears to have been the precursor of the extant white rhino. As diagnosed by Hooijer and Patterson (1972), the cranium differs from that of *C. simum* (Burchell, 1817) by the greater concavity of skull roof, cranium less extended posteriorly, occiput more vertically inclined; cheek teeth not as hypsodont, loph and lophids not markedly oblique, anterointernal corners of upper teeth not rounded, no medifossettes in P²-M² and no fossettids in lower cheek teeth, internal cingula in upper cheek teeth variable. *Ceratotherium praecox* has been recovered from throughout the Kanapoi sequence.

The holotype of *C. praecox* is a relatively complete cranium from Kanapoi (KP 36; Hooijer and Patterson, 1972) but the Kanapoi material is in general much less well preserved than the abundant material of this species that was subsequently described from Langebaanweg (Hooijer, 1972). Newly recovered material includes KP 30187, an incomplete cranium including part of the left maxilla with dP²⁻³, part of the anterior cranial vault with anterior part of left zygomatic arch, and the occiput dorsal to the foramen magnum. The specimen displays primitive characters for *Ceratotherium* in that the occiput is still vertical and not backwardly inclined as in *C. simum*, the posterior part of the cranial vault is flat and rising upward as in *Diceros*, and although the length from the orbit to the nuchal crest cannot be measured because the bone is not continuous it was evidently much greater than in the Lothagam examples of *Diceros*. The premolar lophs are more transversely oriented than in the extant *C. simum*.

Diceros Gray, 1821

Diceros bicornis (Linnaeus)

(Figure 14; Table 16)

KANAPOI MATERIAL. 30216, Lt. P²; 30472, Lt. P³; 40, max frags (Lt. dP³); 39, Rt. humerus.

As at most Pliocene and Pleistocene sites in sub-Saharan Africa, *Diceros* was not a common element of the Kanapoi biota but it is represented by several isolated teeth and a nearly complete right humerus. Older *Diceros* material has been recovered from the Upper Nawata and Apak Members at Lothagam.

The presence together of *Ceratotherium praecox* and *Diceros bicornis*, the latter being less common, is characteristic of Pliocene and early Pleistocene sites in East Africa. *Brachypotherium lewisi* Hooijer and Patterson, 1972, persists into the Apak Member at Lothagam but has not been found at Kanapoi or in the temporally equivalent Kaiyumuung Member at Lothagam.

Family Equidae

Subfamily Equinae

Hipparionine horses of the genus *Hippotherium* von Meyer, 1829, first appear in Africa between 10 and

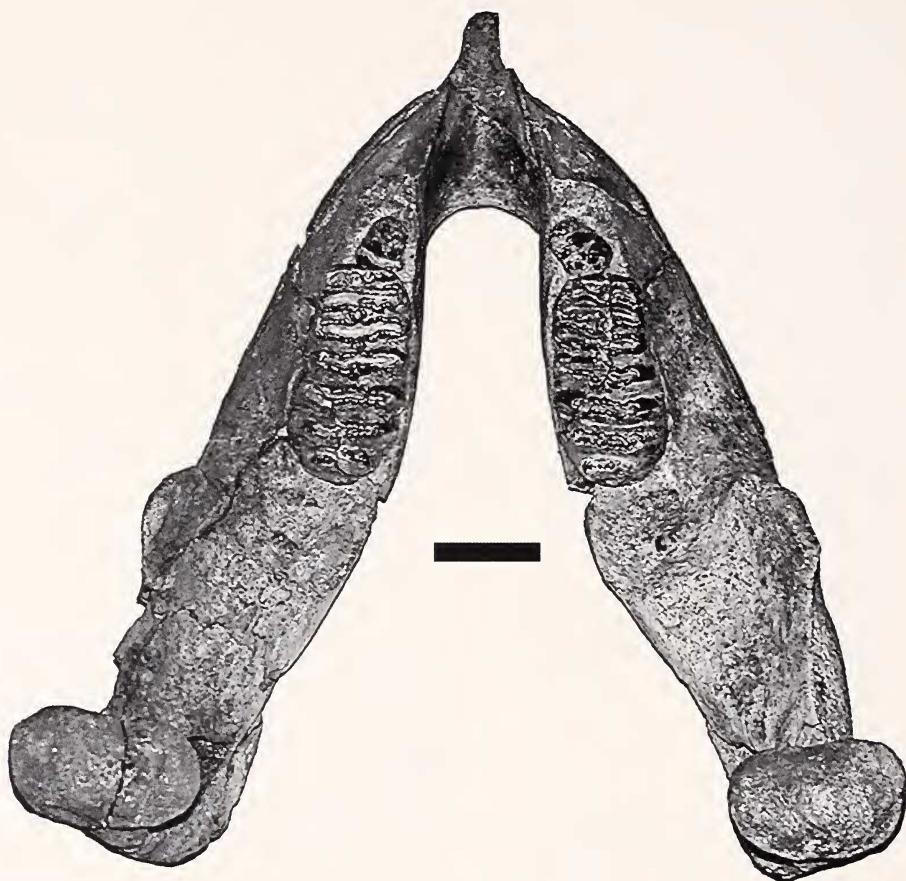


Figure 12 KNM-KP 30616; *Loxodonta adaurora* mandible with Lt. and Rt. P₃, P₄, occlusal view; scale = 5 cm

11 million years ago. A second wave of migration, this time of the genus *Eurygnathohippus* van Hoepen, 1930, took place about 7 million years ago (Bernor and Harris, 2003). Equid material retrieved from Kanapoi represents only the latter genus.

Eurygnathohippus van Hoepen, 1930

As pointed out by Bernor and Harris (2003), all African hipparions of the genus *Eurygnathohippus* are united by the synapomorphy of ectostylids on the permanent cheek teeth. Eurasian and North American hipparions lack this character except in extremely worn hipparion teeth from the late Miocene Dinotheriensandes locality of Germany. *Stylobipparion* van Hoepen, 1932, is the junior synonym of *Eurygnathohippus* by year priority.

Eurygnathohippus sp. indet. (Tables 17, 18)

KANAPOI MATERIAL. 42, Rt. M₃; 43, Lt. P₂, P₄, M₁, Rt. P₂–M₃; 44, Lt. mandible frag (P₃–M₃); 45, m/t frag; 46, Rt. M₁ and tooth frags; 47, Lt. P₃, M₃; 48, Rt. M₁; 49, Lt. and Rt. M₂–₃; 50, M frags;

51, Lt. P₃; 52, Lt. P₃ and /M frags; 53, Rt. P₃; 54, enamel frags; 55, Lt. M₂ and /M frag; 56, Lt. P₃; 57, Lt. P₃; 58, Lt. M₁₋₂; 470, M/ frag; 503, enamel frags; 508, magnum; 518, M frag; 532, Lt. mandible frags (P₂₋₃, M₁₋₃); 544, Lt. M₁; 30167, dist m/p; 30218, Lt. M₁₋₂ and tooth frags; 30220, Rt. M₃; 30473, Rt. M₁ frag; 30476, Rt. P₂; 30493, M frags; 30555, Lt. P₃ and M₃; 30556, Rt. P₃–M₁; 30560, M/ frags; 32809, dl/.

Hooijer and Maglio (1974) recognized three equid species from Kanapoi and Lothagam that they identified as *Hipparion turkanense* Hooijer and Maglio, 1972, *H. primigenium* von Meyer, 1829, and *Hipparion* cf. *H. sitifense* Pomel, 1897. Bernor and Harris (2003) reviewed the Lothagam equids and recognized two common species from the Nawata Formation—*Eurygnathohippus turkanense* and the smaller *E. feibeli* Bernor and Harris, 2003. They also attributed a few postcranial elements to *Hippotherium* cf. *H. primigenium*. Bernor and Harris noted the great variation in tooth morphology in the equid teeth from Lothagam and recommended against naming Pliocene equids from East Africa that were younger in age

Table 13 Kanapoi *Loxodonta adaurora* upper teeth measurements

Accession No.	30150	406	406	28441	383A	
Tooth	RP ²	RM ¹	RM ²	M ²	LM ³	
No. plates	3				9	
No. plates/wear	3				2	
Length	19.31				273	
Length wear surface	16.38			101		
Width (widest plate)	16.77	69.19	72.71		121	
Height (middle plate)					109	
Enamel thickness		4.83		3.5	5.27	
Laminar frequency	20E	5E	4.5	4	3.5	
Accession No.	383B	383C	383E-J	385	385	389
Tooth	RM ³	RM ³		RM ³	LM ³	M ³
No. plates	9	9	9	10	10	
No. plates in wear	7	2	6	8	8	
Length	238+	284		242	234	
Length wear surface	215+	96		189	185	
Width (widest plate)	119	116	110	105.6	108	
Height (middle plate)	94+	117				
Enamel thickness	4.51	4.48	4.48	4.69	4.42	4.23
Laminar frequency	3.5	4		3.5E	3.5	3.5
Accession No.	390	390	30188	30191	30204	
Tooth	RM ³	LM ³	RM ³	LM ³	LM ³	
No. plates	10		8		9+	
No. plates in wear	9		8		4+	
Length	287+		260	265+	250+	
Length wear surface	261+				125+	
Width (widest plate)	107+				110	
Height (middle plate)					91e	
Enamel thickness	6.22	4.03	3.54	7.02	4.18	
Laminar frequency	3.5	3.5	3.5	3.5	3.5	
Accession No.	30204	30596				
Tooth	RM ³	LM ³				
No. plates	9+	7+				
No. plates in wear	4+	7+				
Length	244+					
Length wear surface	130+					
Width (widest plate)	109	120				
Height (middle plate)	85e					
Enamel thickness	4.06	4.5				
Laminar frequency	4	3				

than the Nawata Formation until appropriately complete diagnostic material had become available. This recommendation seems pertinent for the Kanapoi equid hypodigm—given the complete absence of cranial material and that the majority of Kanapoi equids comprise isolated teeth or tooth fragments. A few specimens (KP 48, 51, 53, 57) seem a little larger than most while two specimens (KP 49, 30220) seem a little smaller, but it would be unwise to speculate whether such minor differences are meaningful taxonomically.

Order Artiodactyla

Family Hippopotamidae

The earliest known representatives of this family constitute teeth from middle and late Miocene sites in Kenya and Tunisia that are assigned to the genus *Kenyaipotamus* Pickford, 1983. The extant representatives constitute the dwarf hippo *Hexaprotodon liberiensis* Morton, 1849, from West Africa and the common hippo *Hippopotamus amphibius* Linnaeus. *Hexaprotodon* is the first extant

Table 14 Kanapoi *Loxodonta adaurora* and *L. exoptata* lower teeth measurements

Accession No.	30616	30616	381	381	391	406
Tooth	RP ₃	RP ₄	LM ₁	RM ₁	LM ₁	RM ₁
No. plates	x2x	7	6+	6+	4+	5+
No. plates in wear		6	6+	6+		5+
Length	32.4					
Length wear surface		106				
Width (widest plate)	24.4	53.4	70.44	72.98	70	70
Height (middle plate)	17.5				66	
Enamel thickness		2.4	4.1	4.2	3.7	4
Laminar frequency		7	5	5	4.5	5
Accession No.	396	403	406	32542	32542	
Tooth	RM ²	LM ₂	RM ₂	RM ₂	LM ₂	
No. plates			6+	4+	4+	
No. plates in wear		4+	1+	4+	4+	
Length				89.36	96.75+	
Length wear surface				89.34	96.74	
Width (widest plate)	85.03	90.17	76	80.4	84.4	
Height (middle plate)			81+			
Enamel thickness	4.25	5.81		4.18	5.55	
Laminar frequency	4.5E	4	4.5	4	4	
Accession No.	385 (type)	385	403	407		
Tooth	LM ₃	RM ₃	LM ₃	RM ₃		
No. plates	11	11		11		
No. plates in wear	8	9		5		
Length	279.4	276		289		
Length wear surface	212.4	228		165		
Width (widest plate)	103	100.4	93.37	100+		
Height (middle plate)			98.92	101		
Enamel thickness	4.39	5.12		3.73		
Laminar frequency	4	3.5		4		
Specimen No.	30193	30654	30611 (= <i>L. exoptata</i>)			
Tooth	LM ₃	RM ₃	RM ₂			
No. plates	8+	11	8			
No. plates in wear	7+	11	8			
Length		295	173.6			
Length wear surface			158E			
Width (widest plate)	96	110	71.88			
Height (middle plate)						
Enamel thickness	5.5	4.98	3.58			
Laminar frequency	3.5	3.5	5			

genus to occur in the fossil record. Two species have been documented by Weston (2003) from the late Miocene of Lothagam—*Hex. harvardi* Coryndon, 1977, and *Hex. lothagamensis* Weston, 2000. Neither persist into the early Pliocene of Kanapoi where two hippopotamid species are represented—*Hexaprotodon protamphibius* Arambourg, 1944, which is the common Pliocene hippo from the Lake Turkana Basin, and a smaller unnamed species.

Hexaprotodon Falconer and Cautley, 1836

Hexaprotodon protamphibius
(Arambourg, 1944)

(Figure 15; Tables 19–21)

KANAPOI MATERIAL. 1, Rt. ramus and symphysis; 2, upper premolars; 3, Lt. glenoid; 4, /C frag; 5, mand frag (P₂); 6, Lt. and Rt. mand frags (M_{1–3}); 7, Rt. M₃; 8, symphysis and incomplete ramus; 9, C, I, foot bones; 10, Rt. C/; 11, max frag



Figure 13 KNM-KP 30611; *Loxodonta exoptata*, Rt. M_2 , occlusal view; scale = 5 cm

(Lt. M^{2-3}); 12, Lt. radio-ulna; 13, distal humerus; 14, incomplete forelimb; 15, juvenile Rt. mand ($/C$, dP_4 - M_1); 16, teeth frags; 17, astragalus; 18, Rt. femur; 20, atlas; 21, Rt. $/C$ frag; 22, cranium; 23, ulna; 24, tusk frags and ramus; 25, $C/$; 26, $M/$ and skull frags; 27, P_3 , M_1 , roots dP_4 in ramus; 28, ramus frag (incomplete cheek teeth); 29, incomplete $/M$; 236, tooth frags; 288, Rt. scapula, ribs and vertebra frags; 289, cervical vertebra; 290, thoracic vertebra; 450, Lt. scapula frags; 456, Rt. $/C$; 543, m/p , phalanx; 560, mand; 8690, teeth frags; 8696, mand frags; 8700, femur and ulna frags; 8720, calcaneum and bone frags; 8751, 2nd phalanx; 8752, astragalus; 8753, astragalus; 9910, cranium (M^3 erupting); 30153, mid phalanx; 30209, Rt. M^2 lacking distal portion; 30210, Lt. M_3 , tooth and tusk frags; 30211, Lt. M_2 broken distally; 30224,

Rt. maxilla (M^{1-2}); 30414, astragalus, calcaneum and prox tibia; 30415, P^1 ; 30488, m/p ; 30599, Rt. I_3 ; 30621, $C/$; 30632, Rt. M_1 ; 30638, cranium and mandible; 31737, phalanx (diseased); 32521, M_1 ; 37372, M_3 , $I/$, $/C$.

Hexaprotodon protamphibius was diagnosed by Gèze (1980) as a hexaprotodont or tetraprotodont hippopotamus of medium or submedium size. The skull is relatively narrow with widely separated canine alveoli and orbits little elevated above the facial plane. The lacrimals are enlarged anteriorly and generally separated from the nasals by the persistence of an antorbital process of the frontal. Anterior teeth are small with incisors closely spaced anteriorly; upper canines with deep posterior longitudinal groove; lower canines compressed laterally with finely striated enamel and subparallel

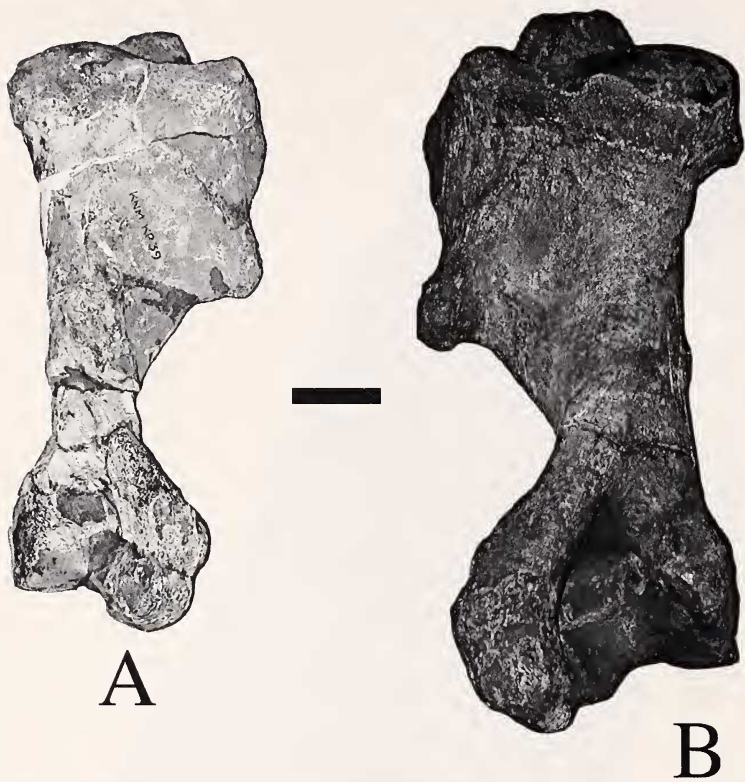


Figure 14 A = KNM-KP 39, *Dicerus bicornis* right humerus; B = KNM-KP 30195, *Ceratotherium praecox* left humerus, posterior view; scale = 5 cm

Table 15 Kanapoi *Ceratotherium praecox* teeth measurements

Upper	30187	Lower	30217	30554	32868	LT 32L	LT 32R
P ¹ ap		P ₁ ap					
ant tr		ant tr					
post tr		post tr					
P ₂ ap		P ₂ ap					
ant tr		ant tr					
post tr		post tr					
P ³ ap		P ₃ ap	40.58			36.69	
ant tr		ant tr	26.74			26.31	
post tr	46.47	post tr				29.01	
P ⁴ ap	48.98	P ₄ ap		46.15	45.69	48E	
ant tr	54.88	ant tr		30.98	28.95	31+	
post tr		post tr		32.11		27.62	
M ¹ ap		M ₁ ap				46.62	
ant tr		ant tr				33.08	
post tr		post tr				33.66	30.78
M ² ap		M ₂ ap				34.41	31.32
post tr		post tr				30.93	32.46
M ³ ap		M ₃ ap					
ant tr		ant tr					
post tr		post tr					

Table 16 Kanapoi *Diceros bicornis* tooth measurements

		41	30216	30472
P ¹	ap	18.94		
	ant tr	21.83		
	post tr			
P ²	ap	29.6	36.04	
	ant tr	33.98	39.37	
	post tr	38.33	41.59	
P ³	ap	36.17		
	ant tr	44.29+		57.23
	post tr	48.23		55.78

Table 17 Kanapoi *Eurygnathohippus* sp. indet. upper dentition measurements

		43	46	47	48	49
P ²	ap	35				
	tr	23.6				
P ³	ap	24.2				
	tr	28.1		27.1		
P ⁴	ap	22.9				
	tr	28.3				
M ¹	ap	22.9	24.5		28.1	
	tr	25	23.7		28.8	
M ²	ap	22.9				20.5
	tr	24.2				19.5+
M ³	ap	23.4		23.8		20.2
	tr	22.1		21.3		18.4

		51	53	57	544
P ²	ap				
	tr				
P ³	ap	26.7	31.3	28.5	
	tr	25	25.2+	25+	
P ⁴	ap				
	tr				
M ¹	ap				25.6
	tr				21.5
M ²	ap				
	tr				
M ³	ap				
	tr				

		30218	30220	30473	30476	30556
P ²	ap				36.9	
	tr				25.8	
P ³	ap					24.4
	tr					24.2
P ⁴	ap					21.8
	tr					23.4
M ¹	ap	23.9		23.6		22.9
	tr					18.8
M ²	ap	23.4				
	tr					
M ³	ap		20.3			
	tr		20			

Table 18 Kanapoi *Eurygnathohippus* sp. indet. lower dentition measurements

		42	44	52	55	56
P ₂	ap					
	tr					
P ₃	ap		27.3	26		25.8
	tr		16.8	16.1		18.6
P ₄	ap		26.7			
	tr		16.2			
M ₁	ap		24.3			
	tr		15.4			
M ₂	ap		25.7		25	
	tr		14.7		15.2	
M ₃	ap	25.2				
	tr	10.4				

		58	532	30555
P ₂	ap		32.1	
	tr		15.1	
P ₃	ap			29.3
	tr		15.8	17.9
P ₄	ap			
	tr			
M ₁	ap	23.5	27.4	
	tr	13.3	14.9	
M ₂	ap	25.6	26.9	
	tr	12.4	15	
M ₃	ap		27.9	28
	tr		12	12

ridges. Cheek teeth are aligned in subparallel rows, brachyodont; premolars simple and with few pustules, lower premolars often with a linguodistal stylid; quadricuspede molars with poorly developed trefoils; simple cingulum sometimes bears styles or stylids. Facial region of the skull is larger than cranial region. The mandible is massive, longer than wide, with horizontal rami incurved beneath the premolars. Limb bones are relatively elongate, articular surfaces more rounded and interarticular crests more salient than in *Hippopotamus amphibius*.

The common hippo at Kanapoi is a small hexaprotodont form of comparable size to *Hexaprotodon protamphibius* from the lower members of the Koobi Fora Formation (Harris, 1991a). Coryndon (1977) assigned Kanapoi hippo material collected by the Harvard University expeditions to *Hexaprotodon harvardi*, but Weston (1997) compared this material to *Hex. protamphibius* and noted the similarity of the Kanapoi specimens both to those from the early part of the Koobi Fora Formation and to those from the lower part of the Shungura Formation that Gèze (1985) had assigned to *Hex. protamphibius turkanensis* (Boisserie, 2002). *Hexaprotodon protamphibius* differs from the earlier *Hex. harvardi* from the Nawata

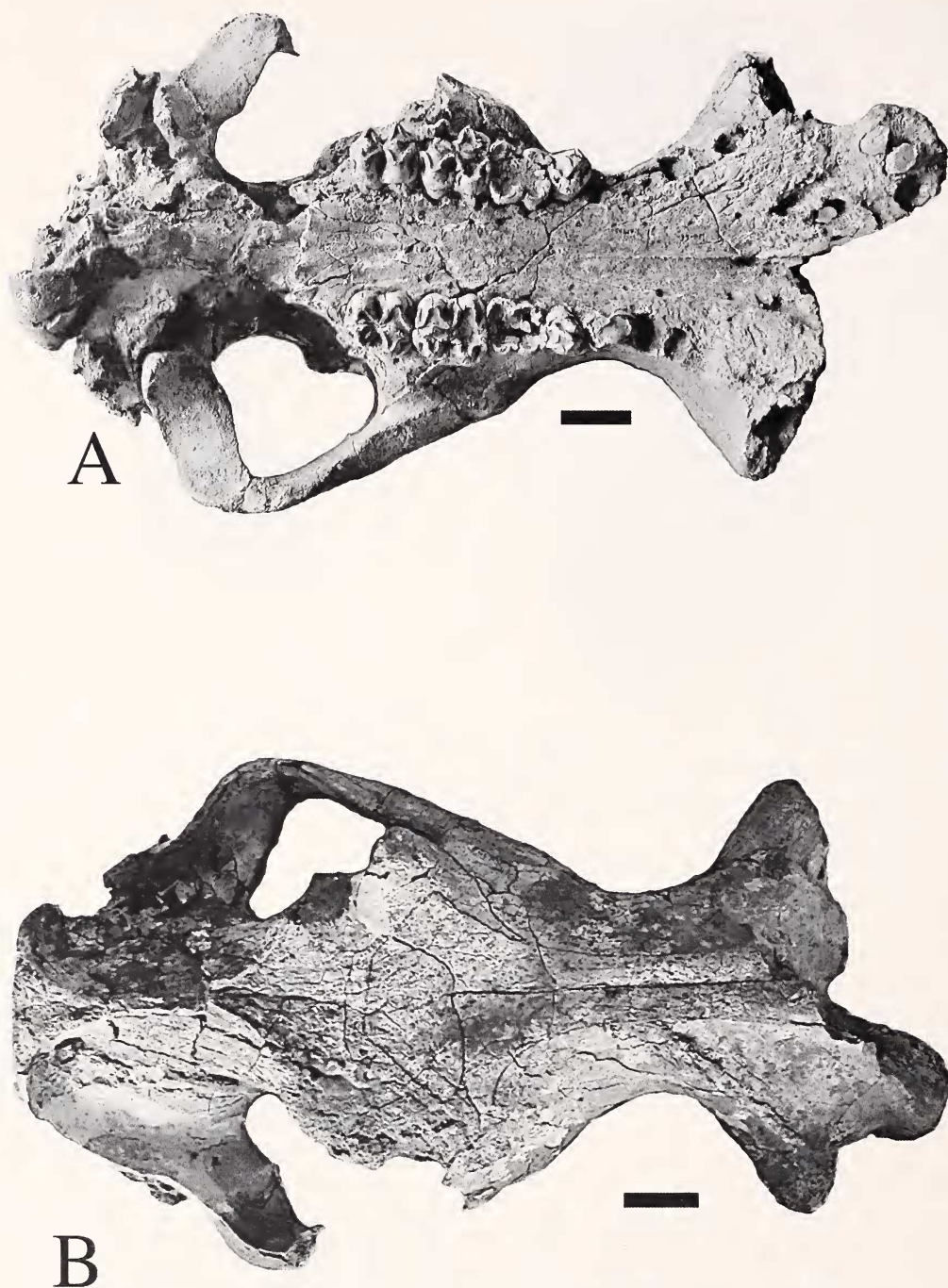


Figure 15 KNM-KP 22; *Hexaprotodon protamphibius* cranium; A = occlusal view; B = dorsal view; scales = 5 cm

Formation and Apak Member of Lothagam because of the size differentiation between the first and posterior incisors (in *Hex. harvardi*, they are of equal size) and by its shorter, stockier limbs (*Hex. harvardi* limbs are larger but more gracile) (Weston 2003). The basicranium is similar to that

of *Hex. harvardi* and the cheek teeth are of comparable size but the occiput is less tall and the palate is wider; the mandible of *Hex. protamphibius* differs from that of *Hex. harvardi* in that the symphysis is longer and wider but less tall and that the tooth row is narrower (Boisserie, 2002).

Table 19 Kanapoi *Hexaprotodon* cf. *H. protamphibius* skull measurements

	22	30638
Length C/ to occipital condyle	560	570
Width at canines	304	330e
Width at P ⁴	141	125
Zygomatic width	373	370

Hexaprotodon cf. *Hex. protamphibius* has been recognized from the Apak Member of the Nachukui Formation (Weston, 2003) and *Hex. protamphibius* persists into the Kalocho Member of the Nachukui Formation (Harris et al., 1988). It is likely that *Hex. protamphibius* gave rise to *Hex. karumensis* Coryndon, 1977, that dominated the latest Pliocene and early Pleistocene aquatic habitats of the Lake Turkana Basin (Harris, 1991a), an interpretation supported by the phylogenetic analysis of Boissarie (2002).

Hexaprotodon sp. indet.
(Figure 16; Table 22)

KANAPOI MATERIAL. 30552, Lt. max with P²–M³.

One maxilla has teeth that are appreciably smaller than the material attributed to *Hexaprotodon protamphibius* but by itself is insufficient to determine whether this is *Hippopotamus imagunculus* Hopwood, 1926, the small hippo common to the Western Rift, or a progenitor of *Hexaprotodon aethiopicus* (Coryndon and Coppens, 1975) the small species present in Plio–Pleistocene horizons in then northern Turkana Basin, or an entirely new species.

Family Suidae

Genera of the suid subfamilies Hyotheriinae, Liotriodontinae, and Sanitheriinae predominated in the early and middle Miocene of sub-Saharan Africa but in the late Miocene were replaced by tetraconodontine immigrants from Asia. *Nyanzachoerus* Leakey, 1958, and the more hypsodont *Notochoerus* Broom, 1925, were characteristic tetraconodontine genera of the latest Miocene and early Pliocene of sub-Saharan Africa. These two genera persist into late Pliocene localities, where they are joined by a second wave of Asian immigrants comprising the suine genera *Kolpochoerus* van Hoepen and van Hoepen, 1932, *Metridiochoerus* and *Potamochoerus* Gray, 1854. The last three genera are not present at Kanapoi.

Nyanzachoerus Leakey, 1958

Nyanzachoerus, as diagnosed by Cooke and Ewer, 1972, and Harris and White, 1979, is a tetraconodontine genus that evidently migrated to Africa from Asia during the late Miocene. *Nyanzachoerus* cheek teeth are similar to those of the extant *Po-*

Table 20 Kanapoi *Hexaprotodon* cf. *H. protamphibius* upper teeth measurements

		2	11	22L	22R
P ²	ap			16.7	
	tr			20e	
I ³	ap			16.4e	
	tr			18e	
P ²	ap	45e			
	tr				
P ³	ap	41e		38	
	tr	29.9		25.6	
P ⁴	ap			35	32
	tr			30.6	31.7
M ¹	ap				
	tr				
M ²	ap		46.8e	50	52e
	tr			47.6	50e
M ³	ap		47.8	47	47
	tr		46.7	45.9	45
		26L	26R	9910	30209 30224
P ²	ap		41.1		
	tr				
P ³	ap		38e		
	tr				
P ⁴	ap	30			
	tr	32.6e			
M ¹	ap				38.4
	tr				40e
M ²	ap	48.7		47.4	45.5 49
	tr	49		48	48.3
M ³	ap	46.7	45.1		
	tr	47.8	47.8		
		30415	30638L	30638R	
P ¹	ap	26.2			
	tr	17			
P ²	ap		39.9		
	tr		32		
P ³	ap		39.7	39e	
	tr		31.8		
P ⁴	ap		34	33.2	
	tr		32.1	32.7	
M ¹	ap		44.4	46.3	
	tr		39	37.8	
M ²	ap		50.5	53.5	
	tr		46.8	46.2	
M ³	ap		51.5	52.1	
	tr		46.4	47.3	

tamochoerus in basic structure but tending to be more hypsodont and with main cusps of molars distinctly more columnar. The third and fourth premolars are relatively larger than in *Potamochoerus*. The upper canines are oval to flattened oval in transverse section, the lower canines verrucose with thin, weakly grooved enamel on two lateral faces. Strong sexual dimorphism is expressed by the size

Table 21 Kanapoi *Hexaprotodon* cf. *H. protamphibius* lower teeth measurements

		1	6R	6L	7	15
I ₁	ap	25				
	tr	25.4				
I ₂	ap	16.1				
	tr					
I ₃	ap	19.4				
	tr	20e				
/C	ap	38				
	tr	58				
P ₁	ap					
	tr					
P ₂	ap	33.4e				
	tr					
M ₁	ap		48.8	48.4		46.7
	tr		34.9	36		33
M ₂	ap	50.7		55		
	tr			43.9		
M ₃	ap	63e			70e	
	tr	37e			37.3	
dP ₄	ap					
	tr					24.8
		27	30210	30211		
P ₂	ap					
	tr					
P ₃	ap					
	tr					
P ₄	ap					
	tr					
M ₁	ap	46.5				
	tr	35.4				
M ₂	ap					
	tr					
M ₃	ap		62.7			
	tr		37	34.5e		
		30599	30632	30638L	30638R	32521
I ₁	ap			27	27.5	
	tr			25	25.5	
I ₂	ap			21.5		
	tr			19.7		
I ₃	ap	20.6		23		
	tr	21.4		21.7		
/C	ap					
	tr					
P ₁	ap					
	tr					
P ₂	ap			35.5	36.9e	
	tr			20.1	20	
P ₃	ap			37		
	tr			23.1		
P ₄	ap			38.9	36.7	
	tr			27	26.9	
M ₁	ap		47	48	49.5	
	tr		35		34.9	
M ₂	ap			52	51.5	50.5
	tr			38	36.5	35.7
M ₃	ap			64	63.5	
	tr			36.9	35.8	

of canines and massiveness of skull. Hollow bony protuberances or bosses are present on the zygomatic arches in males but weak or absent in females. The corpus of the mandible is heavy and contrasts markedly with the unusually thin bone forming the angle.

Nyanzachoerus pattersoni

Cooke and Ewer, 1972

(Figures 17, 18; Tables 24–26)

KANAPOI MATERIAL. 201, Rt. P²–M³; 202, Rt. M₃ broken; 205, Rt. M₁ and M₂; 206, partial Rt. M²; 213, partial Lt. mand (Lt. P₃–M₂, M₃ erupting); 214, frag Lt. max (Lt. P^{3–4}); 215, skeletal elements and tooth frags; 218, Rt. mandible frag (P_{3–4}, M₃ frag; 219, Rt. M₂; 220, broken mand, teeth worn; 221, partial Lt. and Rt. mand rami (milk teeth and Rt. M₁); 222, frag Rt. max (dP⁴, partial M¹); 223, partial skull (Lt. P⁴, M³, Rt. M³); 228, Rt. M₁; 231, facial frag of old male; 232, Rt. M₃ tooth frags; 238, Rt. M₃; 239, female skull and mand (holotype); 240, Lt. and Rt. mand and teeth; 244, subadult skull; 249, mand symph; 255, Lt. mand (Lt. P₄–M₂); 256, Rt. mand (P₄–M₃); 258, mand (Lt. P₄–M₃); 259, Lt. mand (M₂ and M₃); 260, Rt. M²; 261, frag M³, C; 262, skull and mand frags; 263, Lt. and Rt. mand (Lt. P₃–M₃); 264, broken skull and mand (M₃); 266, Lt. juv mand (C, dP₂, M_{1–2}); 273, M³; 275, Lt. mand (P₄–M₃); 329, female cranium and mandible, atlas vertebra, thoracic vertebra; 533, mand frag (M₃); 534, Lt. M₃; 18566, partial skull (Lt. P³–M²); 30159, Rt. P⁴ and M¹ and tooth frags; 30160, female mand (Lt. and Rt. I_{1–2}, C, Rt. P₂–M₃); 30161, male mand (Rt. P₄, M₃, roots Lt. and Rt. I₁/C Rt. P₂, P₄–M₁); 30162, male max (P^{2–4}); 30165, male Lt. and Rt. C/; worn M frag, P²; 30166, Rt. mand (broken M₃), Lt. P₄, condyle, partial M³; 30168, Rt. mand (P_{2–3}); 30177, female mand and symphysis (Lt. and Rt. I_{1–3}, Lt. P_{2–3}, M_{2–3}, Rt. P_{2–4}); 30179, mand (broken M_{2–3}); 30181, M₃ lacking talonid; 30183, mand (M_{2–3}), and frags symphysis; 30186, male cranium; 30203, male mand, skull and tooth frags; 30205, female symphysis (Lt. I_{1–2}), Rt. P₃, P₄; 30267, Lt. and Rt. male mand and symphysis (Rt. /C–M₃, Lt. P₃–M₃); 30268, male broken max and premax (Lt. and Rt. M³); 30271, very broken male skull and teeth; 30403, Rt. mand frag (M₃ and roots M₂); 30409, Lt. mandible (P₄, roots M₁, M_{2–3}), tusk and mand frag; 30410, mand and broken teeth and dist tibia frag; 30411, M³ talonid; 30413, DP⁴ and M¹ and bone frags; 30430, Lt. max (P⁴–M²); 30433, partial skull and teeth; 30453, Rt. P^{3–4}; 30456, M₂; 30458, Lt. M₂; 30462, Rt. M₂; 30474, upper teeth (Rt. P⁴, partial M¹, M², M³); 30475, Lt. mand (P₃–M₂), tooth frags; 30543, molar frags; 30545, I₃; 30547, Lt. mand (dP₄, M_{1–2}); 30551, Rt. mand frags (M₃); 30553, Lt. mand (P₃–M₂), Rt. mand (P₃–M₂) and frags; 30615, P³; 30620, Male Rt. mand (P₄–M₃); 32515, Rt. M³ and tooth frags; 32530, P₂; 32539, Rt. mand (P₄–M₃); 32553, Rt. I₂; 32802, mand (Rt.

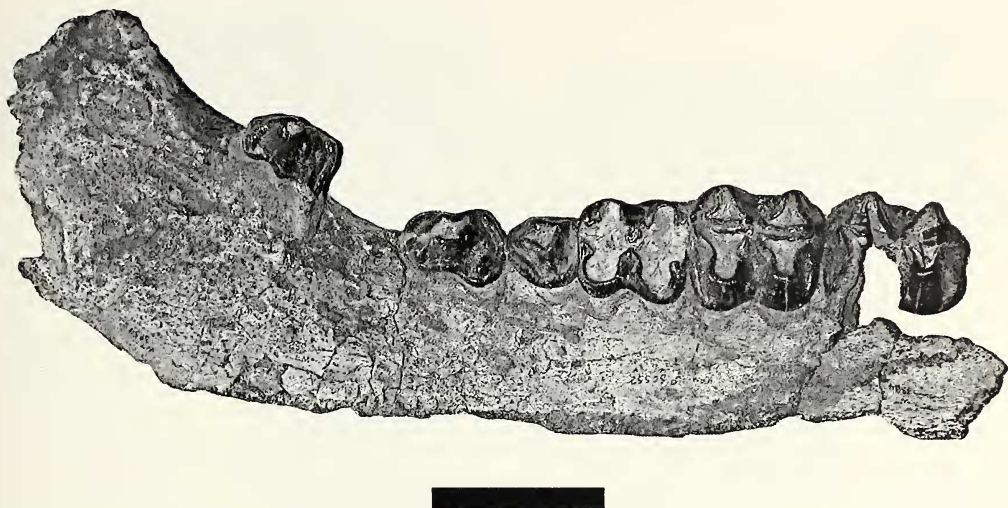


Figure 16 KNM-KP 30552; *Hexaprotodon* sp. indet. left maxilla with P²–M³, occlusal view; scale 5 cm

P₃–M₃); 36841, broken mand (partial P₃, M₁, M₂, M₃) and opp P; 38978, male mandible Rt. /C–M₃, Lt. /C–P₃.

Nyanzachoerus pattersoni is a sexually dimorphic nyanzachoere that is larger than the late Miocene *Ny. syrticus* (Leonardi, 1952) from Lothagam and Sahabi. The first premolars are vestigial or absent. The third and fourth premolars are robust compared with those of *Ny. syrticus* subspecies but are relatively smaller, and the third molars are more elongate and with a more complex talon (id) (Harris and White, 1979). M₃ length is between 48 and 60 mm (van der Made, 1999). The holotype is a female skull from Kanapoi (KNM-KP 239).

Nyanzachoerus pattersoni is the common suid at Kanapoi. Harris and White (1979) interpreted *Ny. pattersoni* as a junior synonym of *Nyanzachoerus kanamensis* Leakey, 1958, but we now consider *Ny. kanamensis* to be a species with narrow premolars

whose distribution was limited to the Western Rift (Harris and Leakey, 2003c). The teeth of *Ny. pattersoni* may be distinguished from those of *Ny. syrticus* and *Ny. devauxi* (Arambourg, 1968) by their larger size, more complex third molar talon(id)s, and proportionately smaller premolars. The third molars are shorter and have less complex talon(id)s than those formerly assigned to “*Nyanzachoerus*” *jaegeri* Coppens, 1971. The teeth display considerable size variation, polarizing between larger male and smaller female specimens. The larger male teeth are only slightly smaller than those of *Ny. australis* Cooke and Hende, 1992, from Langebaanweg, but we think the variation seen in the Kanapoi sample reflects sexual dimorphism rather than the presence of two dentally similar species.

The mandible of *Nyanzachoerus pattersoni* is robustly constructed. The symphysis is relatively narrow across the canine alveoli and moderately concave. The anterior border, which bears three pairs of well-developed and closely proximate incisors, is arched and projects in front of the canines. The concave superior symphyseal surface is deeply excavated in front of the posterior border. The relatively small but stout canines are set at an oblique rather vertical angle. The inferior surface is smooth and only slightly flattened toward the incisive alveoli. The mandible constricts to its minimum width midway along the relatively short postcanine diastema. The posteroventral border merges smoothly with the inferior body of the corpus, which is short, robust, and becomes gradually deeper posteriorly.

At Lothagam, *Nyanzachoerus syrticus* and the much smaller *Ny. devauxi* predominate in the Nawata Formation. The more progressive *Ny. pattersoni* has not been recovered from strata earlier than the Kaiyumung Member although the dentally sim-

Table 22 Kanapoi *Hexaprotodon* sp. upper teeth measurements

		30552
P ²	ap	28
	tr	>22
P ³	ap	31
	tr	25
P ⁴	ap	22
	tr	23.5
M ¹	ap	34
	tr	33
M ²	ap	39.7
	tr	41.1
M ³	ap	42.6
	tr	

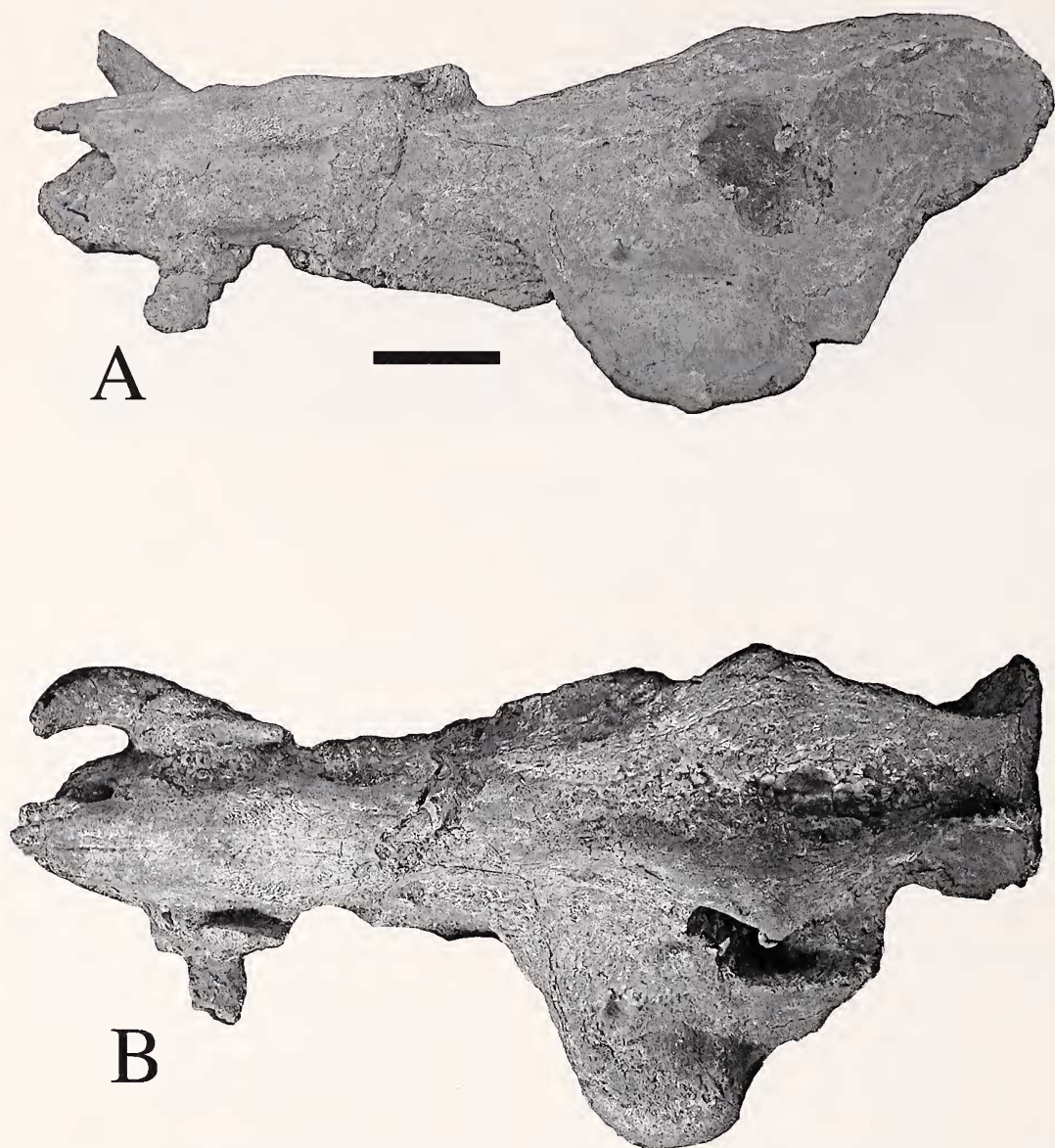


Figure 17 KNM-KP 30186, *Nyanzachoerus pattersoni*, cranium; A = left lateral view; B = dorsal view; C = anterior view. Scale = 5 cm

ilar but somewhat larger *Ny. australis* (Cooke and Hende, 1992) occurs in the Upper Nawata and Apak Members.

Notochoerus Broom, 1925

Notochoerus species are tetraconodontines that have wide and flat mandibular symphyses, small premolars, elongate molars, and very long and hypodont third molars. The M_3 is the longest of all tetraconodontines (van der Made, 1999).

Notochoerus jaegeri (Coppens, 1971) (Figures 19, 20; Tables 24, 27, 28)

KANAPOI MATERIAL. 203, C/ frag; 225, broken Rt. M^3 and partial Lt. M^3 ; 209, partial M_3 ; 210, frag Rt. mand (M_3 broken); 211, Lt. M^3 ; 226, damaged mand (broken Rt. M_3 and P_3); 234, Lt. M^3 , frag Rt. M^3 ; 235, mand (Lt. M_3 , broken Rt. P_4 and /C); 241, damaged mandible (Rt. P_3); 242, male skull frags (zygomatic knob); 245, partial M_3 ; 251, partial skull and mand; 252, upper female canines; 253, Lt. M^3 ; 254, Rt. M_3 and tooth frags; 257, partial skull (Lt. and Rt. P^3 – M^3); 265, M^3



Figure 17 Continued

frags; 267, mand; 269, juv mand (dP_{3-4} , M_1); 270, Lt. M_3 ; 26944, Rt. M^3 and tooth frags; 30178, large mand (Lt. /C, Rt. I_{1-3} , Lt. and Rt. P_3-M_3); 30180, Lt. mand (P_3-M_3); 30182, Lt. M_2 , Rt. M_2 ; 30185, tusk frags; 30402, mand (M_{2-3}); 30452, mand (Rt. and Lt. /C- M_3); 30484, M^3 talon; 30550, mand (M_{2-3}); 30617, male skull (Rt. P^3-M^3); 32528, M_{1-3} ; 32801, Lt. mand. frag (M_3).

Notochoerus jaegeri is a large progressive tetraconodontine possessing three pairs of premolars, of which the third and fourth are proportionately smaller than *Ny. syrticus* or *Ny. pattersoni*. The third molar is longer and taller and has more pillars than those of either of the latter taxa. There is a tendency for the molar enamel to be folded. The

cranium and mandible are larger and more elongate than in *Nyanzachoerus* species; strong sexual dimorphism is evident, with the zygomatic swellings more localized but more protuberant in males (after Harris and White, 1979).

Cooke and Ewer (1972) assigned cranial and dental material of a large suid from Kanapoi and Lothagam to their new species *Nyanzachoerus plicatus*, but this taxon proved to be a junior synonym of the species *Nyanzachoerus jaegeri* erected by Coppens in 1971 for suid dentitions from Chad. Known mainly from its teeth, this species was interpreted by Harris and White (1979) to be morphologically and phylogenetically intermediate between, on one hand, nyanzachoeres represented by

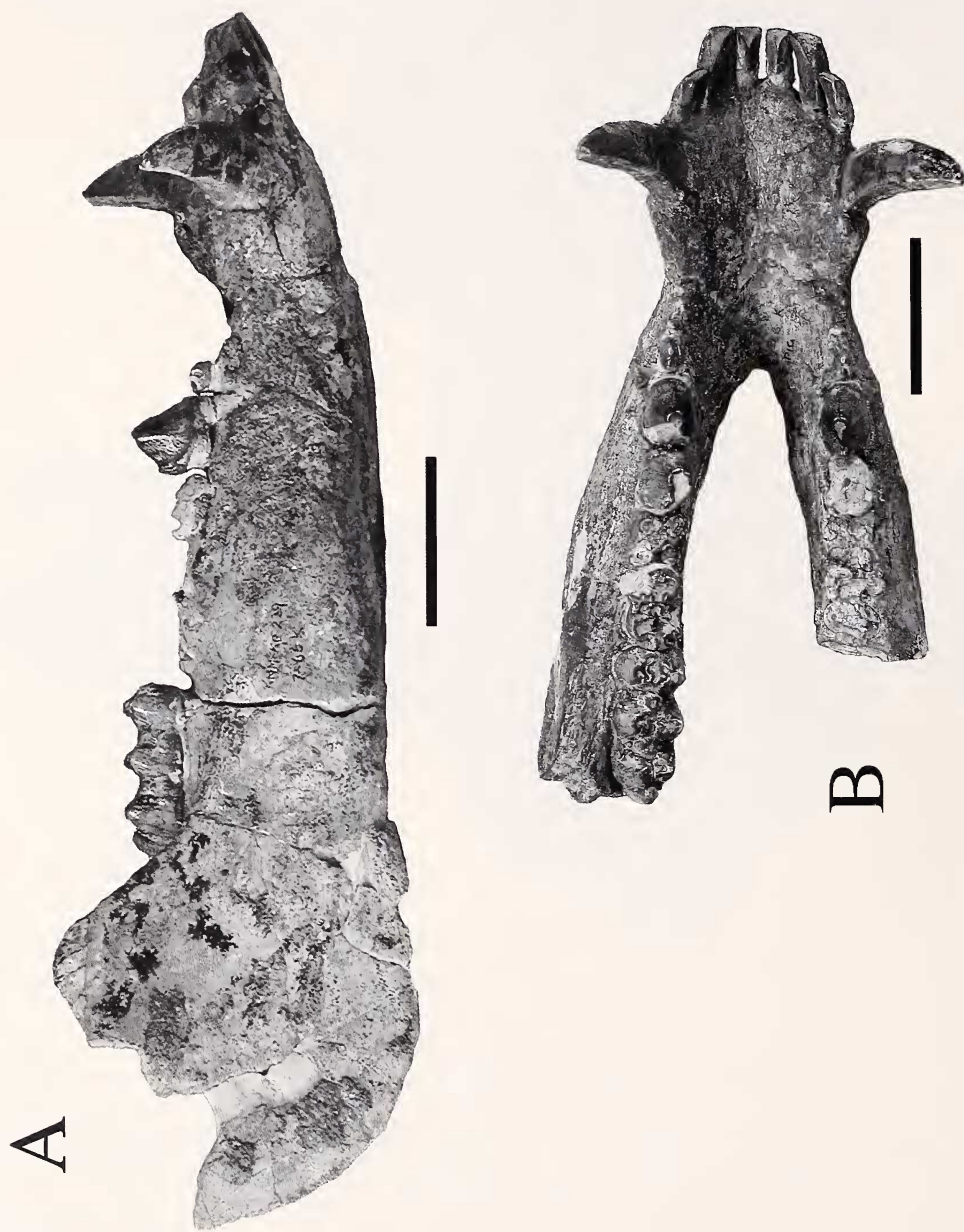


Figure 18 KNM-KP 239, *Nyanzachoerus pattersoni*, mandible; A = right lateral view; B = occlusal view; scales = 5 cm

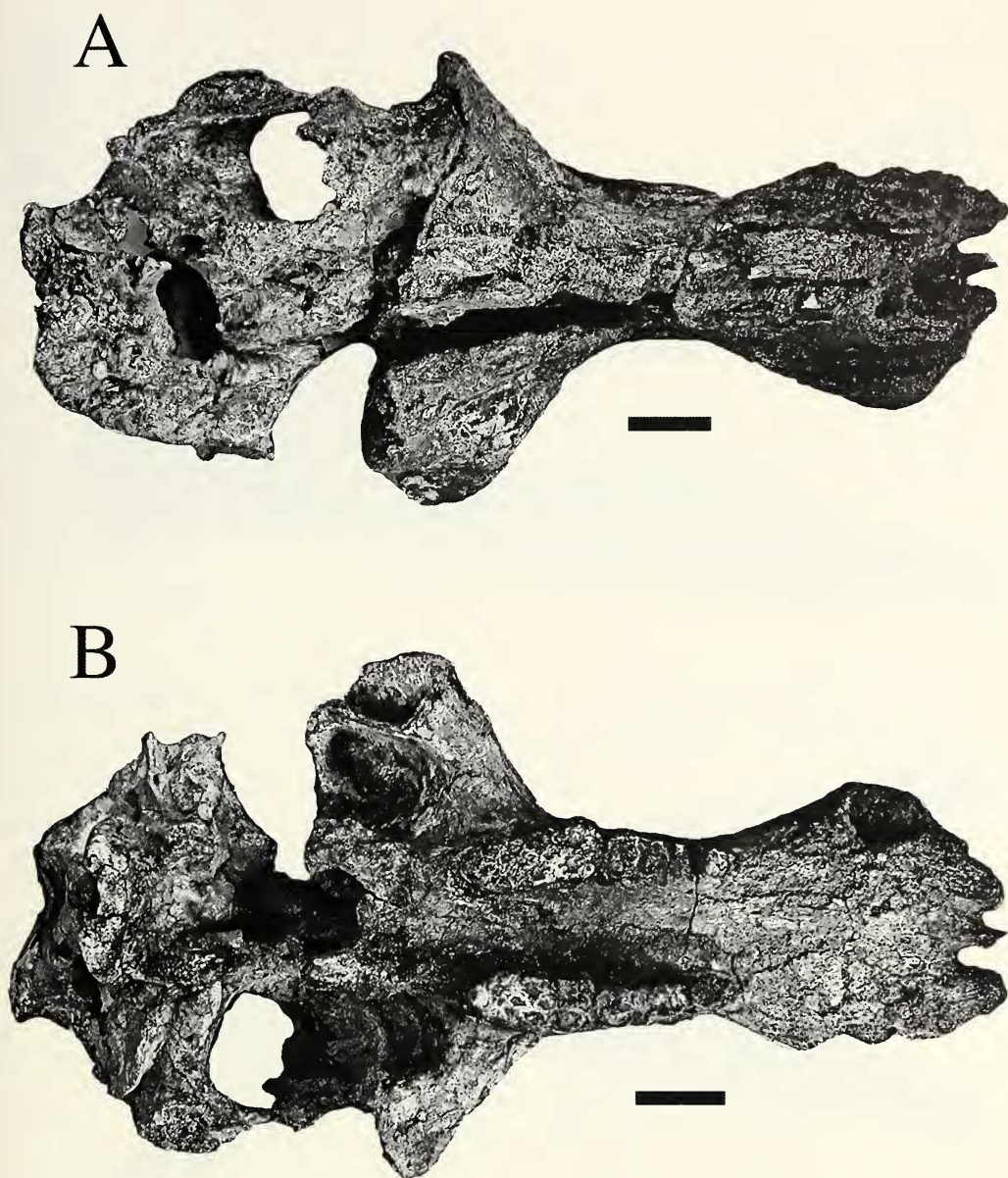


Figure 19 KNM-KP 30617, *Notochoerus jaegeri*, cranium; A = dorsal view; B = occlusal view; scales = 5 cm

Ny. kanamensis and *Ny. pattersoni* and, on the other, the somewhat younger notocherers represented by *Notochoerus capensis* Broom, 1925, from South Africa and *Not. euilus* (Hopwood, 1926), from eastern Africa. New mandibles recovered from Kanapoi by National Museums of Kenya expeditions have augmented our understanding of this species and clarified its phylogenetic relationships.

In contrast with the relatively narrow mandibular symphyses of *Ny. pattersoni* and *Ny. syrticus*, that of *Notochoerus jaegeri* resembles the mandibular symphysis of *Notochoerus euilus* in its breadth and flatness. The corpus of the *Not. jaegeri* man-

dible is longer and less robustly constructed than that of either *Ny. pattersoni* or *Ny. syrticus*. The symphysis is distinctly spatulate and flattened at the widest point across the canine alveoli. The anterior border, which carries three pairs of rather small but well-spaced incisors is almost straight and thickened ventrally at the alveolus. It projects only slightly in front of the anterior edges of the canine alveoli. Behind the canines, the superior surface is less deeply excavated. The large heavy canines extend laterally and anteriorly from their alveoli at a more horizontal angle, curving posteriorly in their distal portions. The inferior surface thins anteriorly

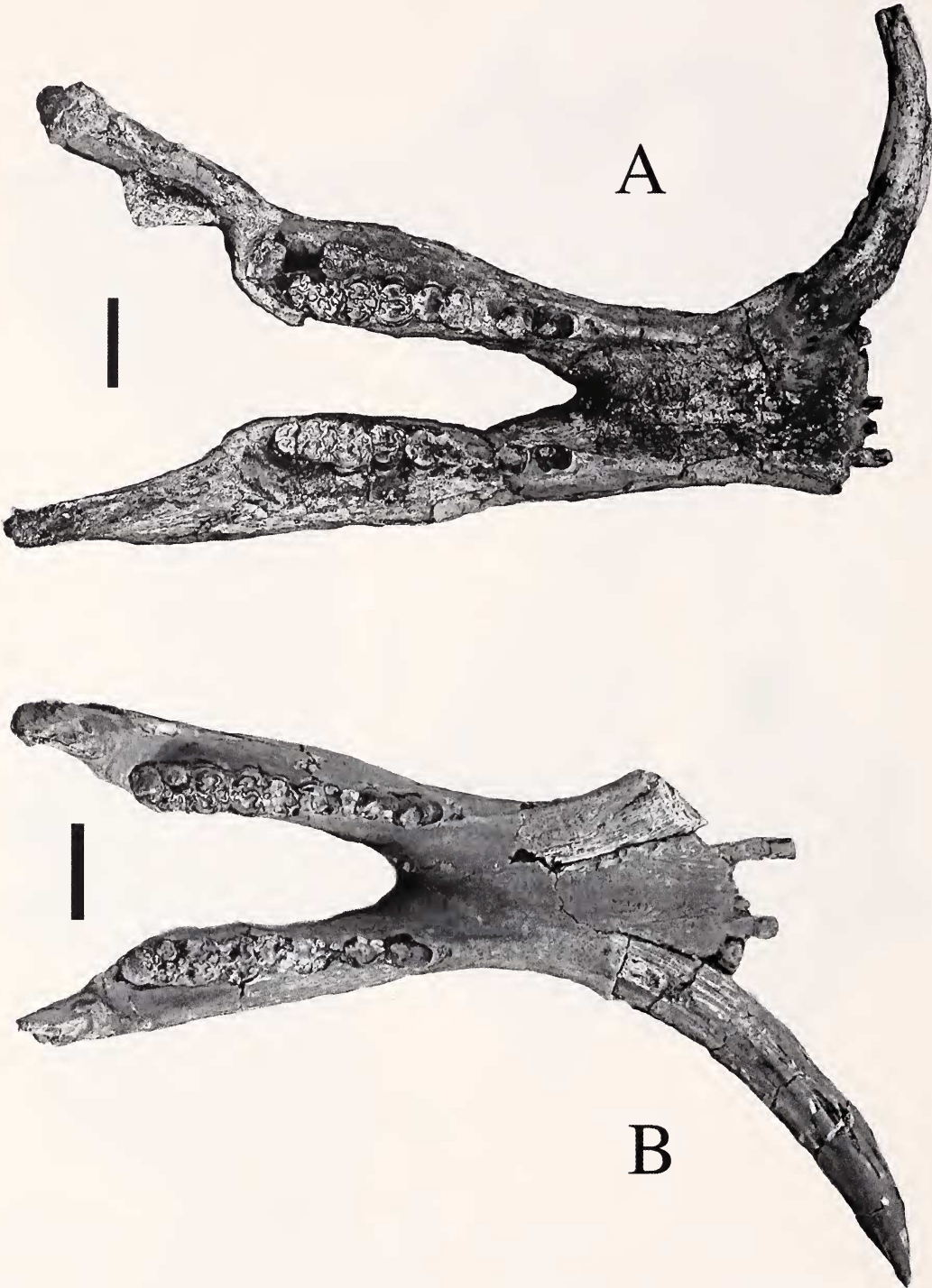


Figure 20 *Notochoerus jaegeri*, mandibles; A = KNM-KP 30178, occlusal view; B = KNM-KP 30452, occlusal view; scales = 5 cm

toward the incisor alveoli and between this and the canines is shallowly excavated either side of the midline. The posteroventral border projects below the inferior surface of the corpus. Posterior to the canines, the mandible constricts to its minimum width midway along the rather long postcanine diastema. The corpus is long, narrow, and relatively lightly built. The inferior surface is elevated between the posterior edge of the symphysis and the angle of the ramus.

The teeth of *Not. jaegeri* resemble a progressive version of *Ny. kanamensis* and *Ny. australis* teeth: the premolars have similar morphology but are proportionately smaller, the molars have similar morphology but the talon(id) of the third molar is more complex. However, the similarity of the orientation of the lower canines and the mandibular morphology to that of *Not. euilus* argues for incorporation of this species in *Notochoerus* rather than *Nyanzachoerus*.

Harris and White (1979) noted tetraconodontine upper third molars from Laetoli that they inter-

preted as primitive for *Not. euilus* on account of their larger size and more massive appearance. Re-comparison of the Laetoli suids with those from Kanapoi suggests that the massive upper molars from Laetoli are better attributed to *Not. jaegeri* than to *Not. euilus*. *Notochoerus jaegeri* is also present in the Apak Member at Lothagam (Harris and Leakey, 2003c).

Notochoerus euilus (Hopwood, 1926)

Notochoerus euilus is a species of *Notochoerus* with a deep and narrow cranium bearing sexually dimorphic zygomatic knobs. The M^3 has two strong lingual talon pillars. The M_3 typically has three pairs of talonid pillars plus single midline terminal pillar or series of pillars. Individual major lateral pillars of molars are moderately tall, widely separated from adjacent lateral pillars, and taper sharply from their bases (Harris and White, 1979).

Table 23 Kanapoi Suidae cranial measurements

	<i>Nyanzachoerus pattersoni</i> 30186 M	<i>Notochoerus jaegeri</i> 30617
Width canine flanges	136	110.3
Width canine alveoli	160	
Nasal boss width	70	
Bizygomatic width	400	
Width postorbital processes	140	
Max width occiput	136	
Nuchal crest-foramen magnum	185	133+
Bicondylar width	76	98.5

Table 24 Kanapoi Suidae mandible measurements

<i>Nyanzachoerus</i> mandibles					
	<i>N. pattersoni</i> M 220	<i>N. pattersoni</i> 239	<i>N. pattersoni</i> 30161	<i>N. pattersoni</i> 30410	<i>N. pattersoni</i> 38978
Length symphysis	144+	118	124	126	140+
Width at canines		75	77.7		110+
Width at I_3	76	61	62		78+
Length P_3 - M_3	153	138	149.6	157	145
Length P_{3-4}	48.3	44.6	51.8	48.6	44
Min width diastema	73	55	52.8	60.2	63
<i>Notochoerus</i> mandibles					
	<i>N. euilus</i> M ER3540	<i>N. euilus</i> F KP30184	<i>N. jaegeri</i> M KP226	<i>N. jaegeri</i> M KP30178	<i>N. jaegeri</i> M KP30452
Length symphysis	172	131	189	195	185+
Width at canines	164	103+	178	150.5	148
Width at I_3	85		120.4	88.6	82
Length P_3 - M_3	159	173		180	163
Length P_{3-4}	36	44		46.7	45.2
Min width diastema	63	68	78	85	74

Table 25 Kanapoi *Nyanzachoerus pattersoni* upper tooth measurements

		201R	205R	205L	222R	223L
P ²	ap					
	tr					
P ³	ap	23.85				
	tr	19.13				
P ⁴	ap					19.97
	tr					22.31
M ¹	ap					
	tr			16.99	16.7	
M ²	ap	28.69		30.93		
	tr			24.27		
M ³	ap	49.71				49.99
	tr	29.62				33.69
dP ³	ap					
	tr		12.78	12.34		
dP ⁴	ap		19.62	15.82		
	tr		14.47	18.01		

		239L	239R	244L	244R	260
I ¹	ap		18.8			
	tr		11.6			
I ²	ap		17.8			
	tr		8.4			
I ³	md					
C/	ap	25.8	22.2			
	tr	16.4	17			
P ¹	ap					
	tr					
P ²	ap	12	7.3	12.36		
	tr	7.1	7	7.65		
P ³	ap	20.5	21.9			
	tr	19.4	18.9			
P ⁴	ap	18.8	17.7	19.31	20.24	
	tr	21.6	20.6	24.49	25.93	
M ¹	ap	18e	20e	20	22.52	
	tr			20.9	20.84	
M ²	ap	26.7	24	32.01	30.64	27.9
	tr	25.3	25	24.68	25.6	20.4
M ³	ap	46.6	47.6			
	tr	34	33.6			

		264L	18566L	30159R	30162R
P ²	ap				10.03
	tr				6.5
P ³	ap				21.89
	tr		19.17		18.48
P ⁴	ap		20.22	18.3	17.47
	tr		23.45	22.5	21.7
M ¹	ap		17.98	18.3e	
	tr			19.5e	
M ²	ap		28.51		
	tr		28.51		
M ³	ap	50.72			
	tr	31.24e			

Table 25 Continued

		30177	30177L	30177R	30268L	30268L
C/	ap	26.5				
	tr	15.4				
P ¹	ap					
	tr					
P ²	ap					
	tr					
P ³	ap		22.27	22.54		
	tr		21.53	22.56		
P ⁴	ap		18.51	18.91		
	tr		21.96	23.2		
M ¹	ap				21.08	
	tr				17.62	
M ²	ap					
	tr					
M ³	ap				51.89	51.5e
	tr					

		30268R	30413	30433L	30433R	30453R
P ²	ap			12.1		
	tr			7.9		
P ³	ap			22	22.3	23.7
	tr			21.5	20.7	
P ⁴	ap			19	18.4	18.7
	tr			23.7	24.3	23.2
M ¹	ap		21.8	15.7e	15.7e	
	tr		19.9	20.7	18.4e	
M ²	ap			26e	27.4	
	tr			24	27.7	
M ³	ap	47.69				
	tr			31.4		28.9

		30474	30615	32515	30474R
P ³	ap	22.1	19.9		
	tr		16.3		
P ⁴	ap				
	tr	22.7			
M ¹	ap				
	tr				
M ²	ap	24.9			25.43
	tr	24.8			24.91
M ³	ap	48.4		48.2	49.07
	tr			31.4	

Notochoerus cf. *Not. euilus*
(Figure 21; Tables 24, 29)

KANAPOI MATERIAL. 30184, female mand with symphysis (Rt. P⁴–M₃, roots Lt. and Rt. I₁, /C). One mandible, female from the size of its canines, has a third molar that terminates in a complex of pillars rather than in a fourth pair of pillars, thereby resembling the third molar of *Not. euilus*. The incisors and premolars are small but not as reduced as those of *Not. euilus* from the Lokochot Member at Koobi Fora (Harris, 1983b). At Lothagam, *Notochoerus euilis* is the predominant suid

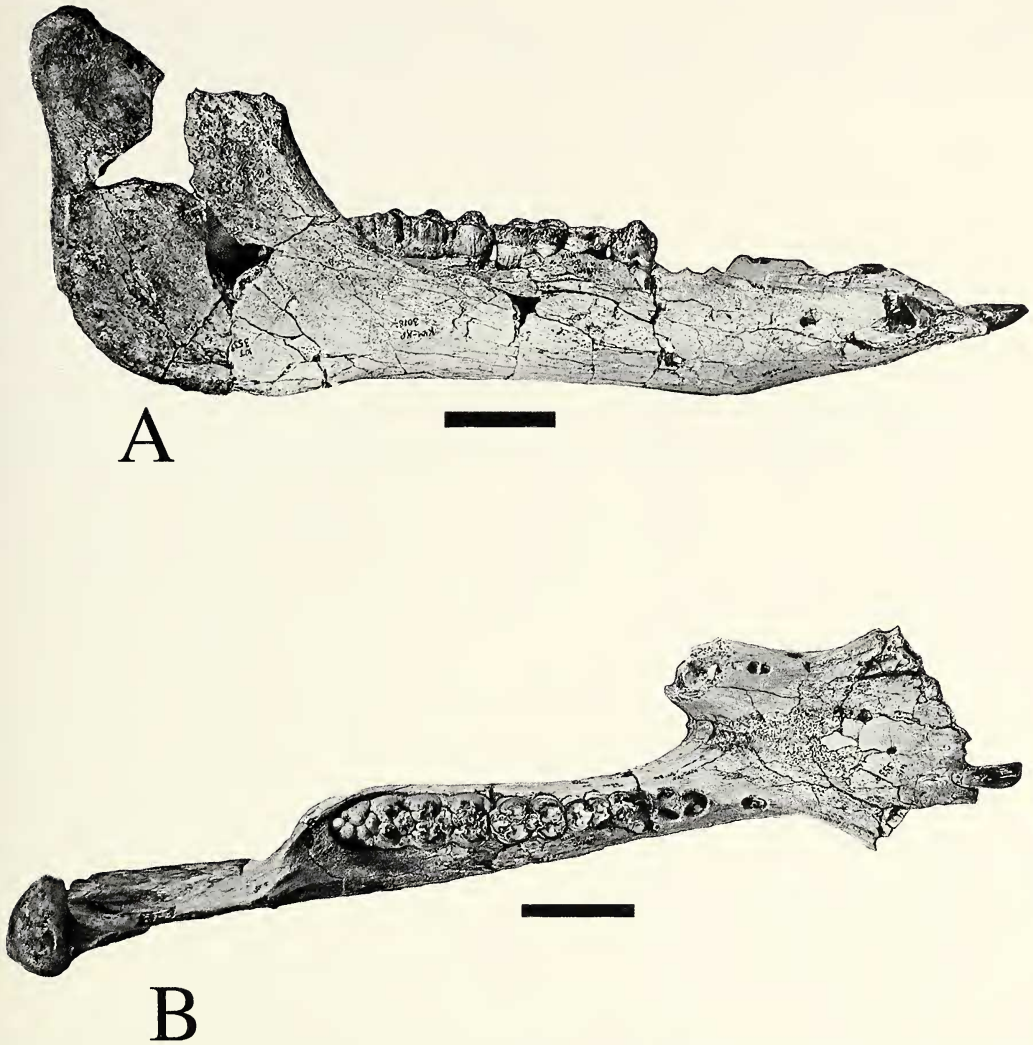


Figure 21 KNM-KP 30184, *Notochoerus* cf. *N. euilus* mandible; A = right lateral view; B = occlusal view; scales = 5 cm

in the Kaiyumung Member but there is a canine from the Apak Member that may also belong to that species.

Family Giraffidae

Giraffoids are rare elements of middle Miocene faunas in East Africa, being best represented by *Climacoceras africanus* MacInnes, 1936, at Maboko, *Climacoceras gentryi* Hamilton, 1978, at Fort Ternan, and *Palaeotragus primaevus* Churcher, 1970, from Fort Ternan and Ngorora (Hamilton, 1978). *Palaeotragus germaini*, first described from late Miocene localities in North Africa (Arambourg, 1959), has been reported from Lothagam (Churcher, 1979), as has a second smaller *Palaeotragus*, species (Harris, 2003a). *Palaeotragines* are not found at African Pliocene localities, their place be-

ing taken by more derived sivatheriines (*Sivatherium* Falconer and Cautley, 1832) and giraffines (*Giraffa* Brunnich, 1771), both probably being derived from Eurasia immigrant stock (Harris, 2003a).

Giraffa Brunnich, 1771

Giraffa stillei (Dietrich, 1942) (Table 30)

KANAPOI MATERIAL. 30151, Rt. $M^{2.or3}$; 30428, Rt. P^4 and M_1 ; 30635, Lt. P_2 ; 30636, Rt. $M_{1.or2}$; 30637, upper tooth frags.

Giraffa stillei is a small species of *Giraffa* with teeth that are often smaller than those of *G. camelopardalis* (Linnaeus, 1798) and *G. jumae* Leakey, 1965, but always larger than those of *G. pyg-*

Table 26 Kanapoi *Nyanzachoerus pattersoni* lower teeth measurements

		202R	213L	215	219R	220R	
P ₂	ap					10.87	
	tr					7.55	
P ₃	ap			24.56		28.31	
	tr			19.47		22.28	
P ₄	ap			21.78	22.11	24.48	
	tr			19.5		22.75	
M ₁	ap						
	tr						
M ₂	ap			27.79	28.68	28.85	
	tr			21.69	22.78		
M ₃	ap		52.88	49.77		56.61	
	tr	24.04	25.19	25.21		28.61	
		221R	228	228L	236L	239L	
I ₁	ap					8.9	
	tr					12	
I ₂	ap					12.3	
	tr					14.6	
I ₃	ap					10.2	
	tr					10	
/C	ap					19.9	
	tr					13.2	
P ₁	ap						
	tr						
P ₂	ap					10.9	
	tr					6.6	
P ₃	ap			27.52			
	tr			24.46		16.8e	
P ₄	ap			26.38			
	tr				20.45		
M ₁	ap	21.79	19				
	tr	13.62	13.9				
M ₂	ap			32.16	31.41	23.7	
	tr			25.99			
M ₃	ap					52.8	
	tr					23	
		239R	240L	240R	255L	256R	258L
I ₁	ap	8.7					
	tr	11.7					
I ₂	ap	10.9					
	tr	13.4					
I ₃	ap	10.6					
	tr	8.7					
/C	ap	21.5					
	tr	13.4					
P ₁	ap						
	tr						
P ₂	ap	11					
	tr	6.7					
P ₃	ap	22.8					22.74
	tr	17					19.88
P ₄	ap						
	tr						
M ₁	ap						
	tr						
M ₂	ap		27.27	26.46	26.73		27.41
	tr		19.81	20.45	20.8		21.11
M ₃	ap	53.3		54.62		53.87	60.17
	tr	22.9		24.05		23.78+	25.32

Table 26 Continued

		259L	260R	260R	262L	263L	264L
P ₂	ap						11.26
	tr						7.78
P ₃	ap			23.26			26.62
	tr			19.78			20.69
P ₄	ap			20.61			23.71
	tr			19.4			21.58
M ₁	ap		19.87	19.21		19.5	
	tr		13.64	14.5		13.18	
M ₂	ap			25.98	33.73	26.19	27.64
	tr			20.14	25.8	18.06	
M ₃	ap	54.21		48.79			56.32
	tr			22.53			28.86
		266L	533R	534L	30160	30161	
I ₁	ap				13.4		
	tr				15.6		
I ₂	ap				12.4		
	tr				17.4		
I ₃	ap						
	tr						
/C	ap				22.8		
	tr				15.3		
P ₁	ap						
	tr						
P ₂	ap				8.2		
	tr				7.5		
P ₃	ap				27.3	24.7	
	tr				20.9	17.5	
P ₄	ap				24.4		
	tr				21.3		
M ₁	ap						
	tr						
M ₂	ap	24.64			26.4		
	tr	19.39			22.7e		
M ₃	ap			56.48	50.6	49.2	
	tr		25.6	26.72	26.4	25.6	
		30161R	30168R	30177L	30177R	30177R	30179L
I ₁	ap					13.4e	
	tr					10.9	
I ₂	ap					14.7	
	tr					13.8	
I ₃	ap					8.6	
	tr					12.5	
/C	ap						
	tr						
P ₁	ap						
	tr						
P ₂	ap			9.08	9.85		
	tr			8.25	7.78		
P ₃	ap		24.4	25.23	25.71		
	tr		17.5	21.36	19.51		
P ₄	ap	20.7					
	tr	16.3					
M _i	ap						
	tr						
M ₂	ap	24.3					
	tr	19.7					
M ₃	ap	52.9e	48.43				75.67e
	tr	24.1	25.65				

Table 26 Continued

		30183L	30205R	30267L	30267R	30267L		
I ₁	ap		9.1					
	tr		12e					
I ₂	ap		12e					
	tr		13.6e					
P ₂	ap	9.97	8.7					
	tr	7.81	7.42					
P ₃	ap	25.61	27.45	24.84	23.56	25.3		
	tr	19.75	21.03	18.27	18.31	18.2		
P ₄	ap	22.47	22.5	21.78	21.22	22		
	tr	20.34	21.33	18.51	20.06	20		
M ₁	ap				17.83	18		
	tr							
M ₂	ap		26.09		28.1	28.5		
	tr		23.52E		21.31	21.5		
M ₃	ap	54.34	52.16		54.06	54.8		
	tr	24.23	27.64		25.26	24.9		
		30267R	30403	30409	30410L	30410R	30456	
/C	ap	32.3						
	tr	22.9						
P ₁	ap							
	tr							
P ₂	ap	10						
	tr	7.1						
P ₃	ap	25.3			25.0	25.5		
	tr	18.5			17.5	18.7		
P ₄	ap	22.2		23	23.5	22.0		
	tr	19.5		19	20.9e	20.5		
M ₁	ap	19.2			20.8e			
	tr	15.5						
M ₂	ap	28.5		26			26	
	tr	22		19.2			17.1	
M ₃	ap	54.5	50.7e	50e		55.6e		
	tr	24e	23.3	22.6				
		30458L	30458	30462	30475	30475L	30545	
I ₃	ap							10.1
	tr							8.5
/C	ap							
	tr							
P ₁	ap							
	tr							
P ₂	ap	10.32						
	tr	7.12						
P ₃	ap	22.91			26.6			
	tr	18.29			24.4			
P ₄	ap	21.45			26.2e			
	tr	19.64						
M ₁	ap	18.06						
	tr	14.88						
M ₂	ap	27.4	28.9	29	33	30.24		
	tr	21.26	20.8	21.5e	26	19.87		
M ₃	ap	54.43						
	tr	23.94						

Table 26 Continued

		30620	32539	32553
I ₃	ap			13.7
	tr			15.5
/C	ap			
	tr			
P ₁	ap			
	tr			
P ₂	ap			
	tr			
P ₃	ap			
	tr			
P ₄	ap	23.2	21.2	
	tr	20.3	19.1	
M ₁	ap	19.5	18.1	
	tr	15.6	14.6e	
M ₂	ap	27.4	25	
	tr	21.8	19.7	
M ₃	ap	58.7e	50	
	tr		24.3	

maea Harris, 1976. The ossicones are uprightly inserted like those of *G. camelopardalis* but appreciably smaller than male specimens of the extant species and often lack well-developed terminal knobs; they are larger than specimens assigned to *G. pygmaea* but are not backwardly raked like those of *G. jumae*.

Five isolated teeth attributed to *G. stillei* are smaller than those of extant giraffes except for one anterior lower premolar (KP 30365) that is about the same size as that of the extant species.

Giraffa jumae Leakey, 1965

(Table 31)

KANAPOI MATERIAL. 30450, Lt. mandible (P₂-M₃).

Giraffa jumae is a large species of giraffe of similar size to the extant *G. camelopardalis*. The surface of the frontal bone between the external roots of the orbits is nearly flat. The width of the skull roof between the orbits is greater than in *G. camelopardalis*. The longitudinal median section from the posterior edge of the nasals to the lateral ossicone is flat or slightly concave. The lateral ossicones originate immediately above the orbit and project more posteriorly than in *G. camelopardalis*. No secondary bone apposition is known to occur on the lateral ossicones. The median ossicone is poorly developed. The basilar process of the occipital is longer than the external width of the palatal area at M². The ascending ramus of the mandible is wide and stout. The corpus is deep and long, the anterior portion of the corpus being inclined upward from the premolars to the symphysis and then downward in the incisive region.

Only one mandible of *G. jumae* has been recovered from Kanapoi. The lower teeth are somewhat

larger than those of extant giraffes and the anterior premolar (P₂) is significantly larger.

Giraffa sp. indet.

(Table 32)

KANAPOI MATERIAL. 98, distal metacarpal; 480, prox phalanx; 472, Lt. astragalus; 473, Rt. astragalus frag; 30446, prox metacarpal; 42091, Lt. radioulna; 42092, Lt. radioulna, Lt. metacarpal, Lt. cuneiform, Lt. semilunar; 42093, Lt. tibia and Rt. humerus.

None of the postcranials were found in association with teeth or ossicones. All are somewhat smaller than those of extant giraffes and thus are more likely to represent *Giraffa stillei* rather than *G. jumae*.

Sivatherium Falconer and Cautley, 1832

Sivatherium hendeyi Harris, 1976

Sivatherium hendeyi is of similar size and dental morphology as the Asian *S. giganteum* Falconer and Cautley, 1832, and the later African species *S. maurusium* Pomel, 1892, but the posterior ossicones are short, extending laterally and backward from the cranium, and are unornamented by knobs or flanges or palmate digitations. The metacarpals longer than in *S. giganteum* or in Pleistocene specimens of *S. maurusium* (after Harris, 1976b).

Sivatherium cf. *S. hendeyi*

(Table 33)

KANAPOI MATERIAL. 135, Lt. fibula; 30227, upper and lower molar frags; 30449, prox Rt. ossicone frag; 32551, Rt. M/ and Rt. M₃ frags.

The proximal right ossicone fragment is trian-

Table 27 Kanapoi *Notochoerus jaegeri* upper teeth

		211L	225L	225R	234L	
P ²	ap		11.48	11.37		
	tr		7.15	7.42		
P ³	ap	23.01	22.49	21.12		
	tr	20.03E	19.07	19.43		
P ⁴	ap	15.86	19.05	18.38		
	tr	19.21	21.83	21.89		
M ¹	ap					
	tr					
M ²	ap		25.56	23.95		
	tr		26.39	24.36		
M ³	ap		47.22	49.37	66.89e	
	tr		33.45	33.68	32.59e	
dP ³	ap					
	tr					
dP ⁴	ap					
	tr					
		253R	257L	257R	26944	26944L
P ²	ap					
	tr					
P ³	ap		21.83	24.15		
	tr		19.42	18.39		
P ⁴	ap		18.76	16.39		
	tr		20.98	21.37		
M ¹	ap					
	tr					
M ²	ap		30.86	29.79		
	tr		25.14	25.71		
M ³	ap	71.78	63.82	63.77	71.2	72.31
	tr	33.23	35.46	36	36.8	36.99
		30617L	30617R			
P ²	ap					
	tr					
P ³	ap		23.0			
	tr		21.0			
P ⁴	ap	22.3e				
	tr	20.8				
M ¹	ap					
	tr					
M ²	ap	35.8				
	tr	25.9	27e			
M ³	ap	74.0	74.2			
	tr	35e	36.9			

gular in transverse section with convex anteromedial and anterolateral surfaces and a flattened posterior surface. The ossicone has a basal sinus and is massive proximally but tapers above the base. The ossicone is somewhat bovine in appearance and appears to have extended outward and backward at the base but curves medially. The anterior surfaces are marked with deep longitudinal grooves. Compared with ossicones of *S. maurusium*, this specimen is smaller, more gracile, and lacks the lateral bosses. Compared with the horn

cores of the bovin *Simatherium* Dietrich, 1941, the ossicone lacks the strong dorso-ventral compression of the bovin horn core and tapers less gradually distally.

The giraffid tooth fragments assigned to *Sivatherium* are much larger than the teeth in the *G. jumae* mandible.

Harris (1976b) proposed the name *S. hendeyi* for the Langebaanweg sivatheres, which were characterized by ossicones that were shorter and simpler than those of *S. maurusium* from younger sites. Churcher (1978) did not use this name but thought the Langebaanweg sivatheres may represent an ancestral African sivathere population. We now know that Pliocene sivathere metapodials associated with *S. maurusium* ossicones were originally of similar length to those of *S. hendeyi* but underwent a dramatic reduction in length when *S. maurusium* adopted a grazing diet at the end of the Pliocene (Harris and Cerling, 1998; Cerling et al., in press). The Kanapoi ossicone is referred to *S. hendeyi* on the basis of its size and morphology.

Family Bovidae

The family Bovidae is sparsely represented at early Miocene localities in East and North Africa (Hamilton, 1973; Gentry, 1978) but bovids were the most numerous terrestrial mammals at the mid-Miocene site of Fort Ternan (Gentry, 1970) and they dominate younger vertebrate fossil assemblages from eastern Africa. Bovids occur in both Eurasia and Africa during the early Miocene, and thereafter, migrations occurred between them repeatedly (Vrba, 1985, 1995) but Gentry (1990) argues for Africa as the origin of this family. Because the sole apomorphic character characterizing the family Bovidae is the presence of horn cores (Janis and Scott, 1987), it would be difficult to substantiate a hornless bovid ancestor with any degree of certainty.

The Antilopini and Caprini, both of Eurasian origin, are first represented in Africa about 14 million years ago; the endemic Cephalophini and Neotragini make their appearance shortly thereafter. Toward the end of the Miocene, Ovibovini and Bovini migrated into Africa from Eurasia while the endemic Tragelaphini, Hippotragini, Alcelaphini, and Aepycerotini are documented for the first time. The Reduncini, whose continent of origin is uncertain, also appear in the late Miocene whereas the Boselaphini become extinct in Africa near the Mio-Pliocene boundary (Vrba, 1985).

The Kanapoi bovid assemblage is dominated by tragelaphins, alcelaphins, and aepycerotins—suggesting a mixture of open and closed mesic to xeric habitats. Boselaphins, common elements in the Nawata Formation at Lothagam and persisting into the Apak Member (Harris, 2003b), have yet to be recovered from Kanapoi.

Table 28 Kanapoi *Notochoerus jaegeri* lower teeth measurements

		210R	226	235R	235L
P ₂	ap				
	tr				
P ₃	ap				
	tr		13.4		
P ₄	ap			21	
	tr				
M ₁	ap				
	tr				
M ₂	ap				
	tr				
M ₃	ap	80.56			67.66
	tr	27.89			27.06

		241R	267R	251L	251R	252R
P ₂	ap					
	tr					
P ₃	ap	23.86	22.55	23.97	22.48	
	tr	16.71	13.74	16.84	16.78	
P ₄	ap		18.1	19.89		
	tr		15.32	17.18		
M ₁	ap					20.44
	tr					13.81
M ₂	ap					
	tr					
M ₃	ap			64.55	61.18	
	tr			25	25.07	

		267L	269R	30178L	30178R
P ₂	ap				
	tr				
P ₃	ap			25.85	25.55
	tr			17.92	17
P ₄	ap			20.88	
	tr			18.48	17.8e
M ₁	ap		26.6		
	tr		14.05		
M ₂	ap			34.06	35.79
	tr			23.55	24.65e
M ₃	ap	81.97		77.28	80.87
	tr	28.37		30.34	30.37

		30180L	30182L	30402	30550	32258
P ₂	ap					
	tr					
P ₃	ap	23.6				
	tr	16.4				
P ₄	ap	19.7				
	tr	17.1				
M ₁	ap					
	tr	16				
M ₂	ap	31	32			35.6
	tr	22e	20.2+	22.3		23.6
M ₃	ap	70.2		76.6	82	78.9
	tr	24.9		30.3	29+	29.6

Table 28 Continued

		32801	30180L	30182R	30452R	30452L
P ₂	ap					
	tr					
P ₃	ap	23.62		26.61		26.48
	tr	16.49		17.64		
P ₄	ap	19.47		20.68		20.46
	tr	17.11				
M ₁	ap	19.4				
	tr	15				
M ₂	ap		31.78	35.51		29.18
	tr			19.95	21.22	
M ₃	ap	76e	71.99		71.65	71.51
	tr	26e	25.04		23.8	24.7e

Tribe Tragelaphini

Tragelaphus Blainville, 1816

Tragelaphus species are medium to large tragelaphins with spiraled horn cores inserted close together and having an anterior keel and sometimes a stronger posterolateral one; small- to medium-sized supraorbital pits, which are frequently long and narrow, and an occipital surface tending to have a flat top edge and straight sides (Gentry, 1985). The genus *Tragelaphus* is diverse, including the kudus, the nyalas, the sitatunga, and the more ubiquitous bushbuck. Greater and lesser kudu occur today in the northern half of the Turkana Basin.

Tragelaphus kyaloae Harris, 1991

(Table 34)

KANAPOI MATERIAL. 68, occiput; 77, Lt. h/c frags; 78, Lt. h/c frag; 79, Rt. and Lt. h/c frags; 80, Lt. h/c frag; 81, Rt. h/c frags; 82, Rt. h/c frags; 84, dist Rt. h/c frag; 86, Lt. h/c frags; 87, dist Lt. h/c; 88, dist. Rt. h/c frag; 89, dist. Rt. h/c frag; 90, prox

Table 29 Kanapoi *Notochoerus euilus* lower tooth measurements

		30184R
I ₂	md	11.7
	bl	13.6
P ₂	ap	
	tr	
P ₃	ap	
	tr	
P ₄	ap	20.5
	tr	16.7
M ₁	ap	21.0
	tr	14.9
M ₂	ap	32.4
	tr	21.4
M ₃	ap	73.5
	tr	25.8

Table 30 Kanapoi *Giraffa stillei* tooth measurements

		KP 30635	KP 30636	KP 30637A	KP 30637B	KP 30428	30151
P/	ap					18.51	
	tr					16.43	
M/	ap				25.37	21.22+	23.16
	prot			25.41			24.45
	met						21.65
P ₂	ap	15.25					
	tr	10.61					
P ₃	ap						
	tr						
P ₄	ap						
	tr						
M ₁	ap		23.74				
	prot		16.47				
	met		16.64				
M ₂	ap						
	prot						
	met						
M ₃	ap						
	prot						
	met						

Rt. h/c frag; 91, prox Lt. h/c frag; 92, frontlet and prox Rt. h/c; 29258, prox Rt. h/c frag; 29260, prox Rt. h/c; 29261, prox Rt. h/c; 29268, prox Rt. h/c; 29269, dist Rt. h/c; 29272, prox Lt. h/c; 29278, dist Rt. h/c; 30156, h/cs and frontlet; 30158, calvaria and h/cs; 30445, prox Rt. h/c; 30448, h/c frags; 30486, dist. Rt. h/c; 30628, dist Lt. h/c frag; 30629, Rt. h/c frag; 30634, prox Lt. h/c; 32519, prox Rt. h/c frag; 32559, dist. Rt. h/c frag; 29266, dist Lt. h/c.

Tragelaphus kyaloae is a medium-sized tragelaphin with horn cores inserted close together, at a low inclination, that diverge rapidly from their base but converge distally, and that spiral 180° anti-

clockwise in the right horn core. Proximally, there is a strong posterolateral keel and a fainter anterolateral keel; distally, these become anterolateral and posteromedial, respectively. The shape of the horn cores is reminiscent of the extant sitatunga (*T. spekei* Sclater, 1863); they are less helically coiled than in *T. strepsiceros* (Pallas, 1766), *T. imberbis* Blyth, 1869, or *T. gaudreyi* (Thomas, 1884) but converge closer distally than in *T. nakuae* Arambourg, 1941, or the kudu-like species. The cranial vault bears a faint but distinct transverse bar immediately in front of the nuchal crest. The paroccipital processes are short but stout, and the posterior tuberosities of the basioccipital are much wider than the anterior ones.

This is by far the most abundant bovid in the Kanapoi biota. The holotype of *T. kyaloae* is from the lower Lokochot Member at Kosia (Harris, 1991b) and it is the common tragelaphin in the Lokochot and Moiti Members of the Koobi Fora Formation (Harris, 2003b). The oldest documented occurrence of this taxon is a single specimen from the Upper Nawata at Lothagam but it is also represented by a dozen horn cores from the Apak and Kaiyumung Members of the Nachukui Formation at Lothagam. The horn cores are similar in cross-section to those of *T. nakuae*, the common Pliocene tragelaphin of the Lake Turkana Basin, but have more pronounced torsion.

Tragelaphini gen. indet.
(Table 35)

KANAPOI MATERIAL. 32514, Lt. maxilla (P⁴-M³); 66, Rt. mandible (M₂₋₃); 67, Lt. mandible frag (M₁); 76, Lt. M¹; 109, Lt. M¹; 29273, Lt. and Rt.

Table 31 Kanapoi *Giraffa jumae* tooth measurements

		KP 30450
P ₂	ap	20.62
	tr	13.62+
P ₃	ap	25.03
	tr	19.83
P ₄	ap	26.15
	tr	22.17
M ₁	ap	28.81
	prot	
	met	
M ₂	ap	29.76
	prot	22.52
	met	22.62
M ₃	ap	46.42
	prot	23.89
	met	21.56

Table 32 Kanapoi *Giraffa* sp. indet. postcranial measurements

	Specimen	Length	Prox ap	Prox tr	Dist ap	Dist tr	Epic tr
42093	Humerus				119.5	110.42	125.58
42092	Radius		70.43	115.14	66.48	106.77	
42092	Prox ulna			63.31			
98	Metacarpal				61.8	92.15	
30446	Metacarpal		37.43	65.01			
42092	Metacarpal		66.7	97.7	57.63	86.53	
42093	Tibia				76.59	102.95	
480	Proximal phalanx	66.98	33.2	33.15	22.48	27.86	
			Max ap	Max tr	Max dv		
42092	Cuneiform		69.5	35.0	60.5		
42092	Semilunar		61.4	43.5	48.0		

M¹⁻²; 30395, Lt. M¹⁻²; 30396, Lt. M³; 30421, Rt. M₁, Lt. M₂, Rt. M₃; 30441, Lt. M¹; 32545, Lt. mandible frags (P₂-M₁); 32570, Lt. mandible frags, P₃-M₁; 32573, M₁, Lt. M₁, and tooth frags; 32574, Lt. M₁; 32829, upper and lower molar frags; 32881, Rt. P₃; 36861, Rt. mandible (P₃₋₄) and bone frags.

A number of isolated tragelaphin dentitions were recovered. Most are of similar size and presumably represent *Tragelaphus kyaloae* but the smaller KP 32514 indicates that at least two tragelaphin species were present at Kanapoi.

Tribe Bovini

Simatherium Dietrich, 1941

Only one extant bovin species, *Syncerus caffer* (Sparman, 1779), is endemic to sub-Saharan Africa but three other genera—*Ugandax* Cooke & Corydon, 1970, *Simatherium*, and *Pelorovis* Reck, 1928—are represented in the fossil record. *Simatherium* differs from *Ugandax* by being larger and having more widely separated horn cores that are more divergent basally and more curved anteriorly. The more derived *Pelorovis*, is unknown before the late Pliocene. *Simatherium kohllarseni* Dietrich 1942 was originally described from Laetoli in Tanzania whereas the somewhat older *Simatherium demissum* Gentry, 1980, was first described from Langbaanweg in South Africa.

Simatherium demissum Gentry, 1980

Simatherium cf. *S. demissum* (Figures 22, 23; Tables 36, 37)

KANAPOI MATERIAL. 96, Rt. mandible (P₂-M₃) and assoc postcranial; 29265, skull frags, Lt.

maxilla (P²-M³), Rt. maxilla (P⁴, M²⁻³); 30612, broken skull with Rt. and Lt. h/cs; 32560, Lt. M¹ frag.

This Kanapoi bovin is represented by a very battered calvaria with portions of both horn cores and by a partial upper dentition, both collected by National Museums of Kenya parties, and by a mandible and associated postcranial elements that were collected by the Harvard University expedition. The horn cores are strongly dorso-ventrally compressed. They extend outward and backward from their bases but ascend upward toward their tips. The horn cores taper gently in their proximal portion but more rapidly toward their tip. The surface of the horn cores is not well enough preserved to confirm the presence or absence of a lateral keel but are otherwise ornamented by strong longitudinal ridges and furrows. Although the bone is very incompletely preserved, the braincase evidently extended for some distance behind the horn cores and was bordered by well-developed temporal fossae. There was a strong interfrontal crest.

Tribe Hippotragini

There are three extant genera of hippotragins—*Hippotragus* Sundevall, 1846 (roan and sable antelopes), *Oryx* Blainville, 1816, and *Addax* Rafinesque, 1815, and several extinct genera. Vrba (1987) suggested that, early in their history, the hippotragins diverged into two major subclades—one exemplified by *Hippotragus*, with uprightly inserted and mediolaterally compressed horn cores, and the other by the less water-dependent *Oryx* and *Addax*, with horn cores that are less mediolaterally compressed but bent more strongly backwards.

Hippotragini gen. indet. (Figure 24; Table 38)

KANAPOI MATERIAL. 483, B-D, Lt. P⁴-M¹, Lt. M³, Rt. M²; 29274, Rt. mandible (M₂₋₃); 30631, proximal Rt. h/c; 32526, Lt. M¹.

This taxon is represented by the proximal portion of a large right horn core that is mediolaterally

Table 33 Kanapoi *Sivatherium* fibula measurements

	Length	Prox tr	Dv
135	55.79	31.42	33.85



Figure 22 KNM-KP 30612, *Simatherium* cf. *S. demissum*, calvaria, dorsal view; scale = 5 cm

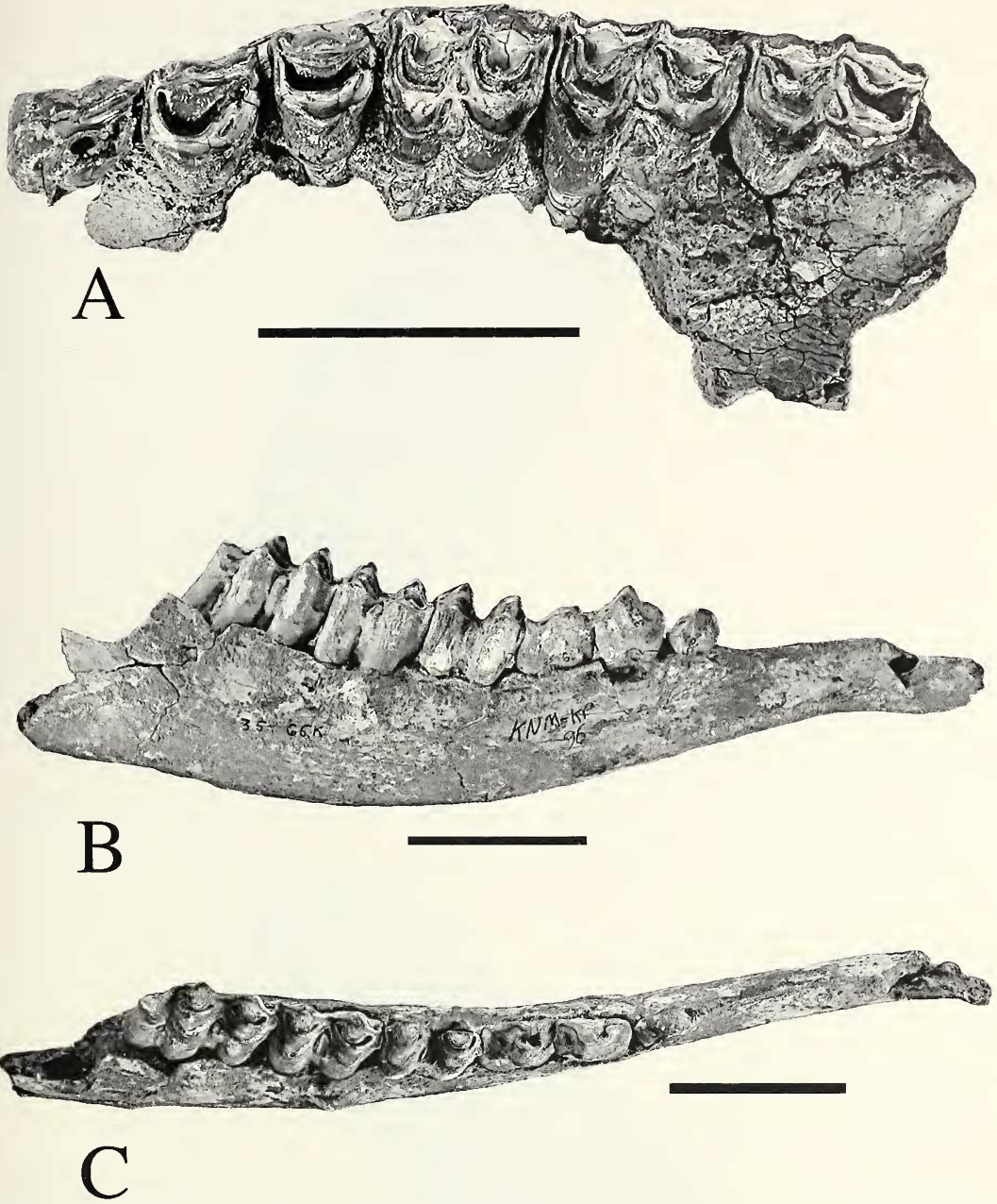


Figure 23 *Simatherium* cf. *S. demissum*, dentitions; A = KNM-KP 29265, left maxilla, dorsal view; B = KNM-KP 96, right mandible (P_3 – M_3), lateral view; C = KNM-KP 96, occlusal view; scales = 5 cm

compressed with a flattened lateral surface. The horn core curves gently backward from its base with a slight lyrate flexure in anterior view. There is faint transverse annulation on the anterior surface. At its base, the horn core measures 46.1 mm anteroposteriorly; the transverse measurement is 33.9 mm.

A few hippotragin teeth were recovered although

none were associated with the sole recognized hippotragin horn core.

Tribe Reduncini

Reduncins are small to large antelopes with hypodont teeth for grazing and today characteristically occur in grasslands near permanent water. There are two extant genera—*Kobus* Smith, 1840 (water-



Figure 24 KNM-KP 30361, Hippotragini gen. indet., proximal right horn core; A = lateral view; B = medial view; scales = 5 cm

Table 34 Kanapoi *Tragelaphus kyaloae* horn core measurements

	prox ap (Rt)	prox tr (Rt)	lt (Rt)	prox ap (Lt)	prox tr (Lt)	lt (Lt)
77				38	53.12+	
78				38	50	
79	41	50				
80				33	44	
81	31+					
86				33	47	
90	37	45				
91				43	56	
92	38	46				
29258	38	49				
29260	40	53				
29261	37	48				
29268				39	51	
29272				38	46	
30156	38	50		38	49	
30158	42	54		41	55	
30445	38	53				
30634	34	52				

bucks, kobes, etc.) and *Redunca* Smith, 1827 (reedbucks). The earliest recognized species of *Kobus* are from Lukeino and Lothagam.

Kobus Smith, 1840

Kobus sp. indet.

KANAPOI MATERIAL. 461, Rt. h/c frags; 29267, proximal Rt. h/c.

KP 29267 is a small but stout horn core that curves backward and slightly outward from its base. The horn core tapers gently upward from its base and the lateral surface is slightly flattened. At its base, KP 29267 measures 35.5 mm anteroposteriorly and 28.2 mm transversely. Corresponding measurements for KP 461 are 34.9 and 28.8 mm. The two horn cores are smaller than those of *K. presigmoidalis* Harris, 2003b, from Lothagam.

Reduncini gen. indet.

(Table 39)

KANAPOI MATERIAL. 75, Rt. P₃; 463, Lt. mandible (M₁); 29275, Rt. maxilla (P⁴-M³); 29276, Rt. mandible (P₂-M₁); 29279, Rt. mandible (P₂, M₁₋₃); 30626, Lt. mandible (P₄-M₁); 27450, Lt. M₁.

A few reduncin teeth were recovered but none were associated with the *Kobus* horn core.

Tribe Alcelaphini

Alcelaphins are represented by four extant genera: *Damaliscus* Sclater and Thomas, 1894, *Beatragus* Heller, 1912, *Alcelaphus* de Blainville, 1816, and *Connochaetes* Lichtenstein, 1814, plus a number of extinct genera. All the extant genera are specialist bulk grazers that are capable of going without water for varying intervals of time. *Damalacra* species

were originally described from Langebaanweg (Gentry, 1980) and the genus was subsequently recognized at Lothagam (Harris, 2003b) and elsewhere. A cladistic analysis of fossil and living Alcelaphini by Vrba (1997) suggested that two alcelaphin subtribes diverged during or before the Mio-Pliocene transition—the Alcelaphina (*Damalacra neanica* Gentry, 1980, and *Beatragus*) and the large clade Damalascina (which includes the *Damaliscus* and *Parmularius* Hopwood, 1934 lineages). Both subtribes appear to be represented at Kanapoi.

Damalacra Gentry, 1980

Damalacra neanica Gentry, 1980

Horn cores of *Damalacra neanica* are without compression or are slightly compressed anteroposteriorly, have no flattened lateral surface, taper fairly sharply from base to tip, show much increased divergence distally, have either slight forward or slight backward curvature in profile, and are inserted behind or above the back of the orbits. The boundary between the pedicel top and the base of the horn core is higher on the medial than on the lateral side of the horn cores. Female horn cores are smaller than those of males, as in extant alcelaphins (after Gentry, 1980).

Damalacra cf. *D. neanica*

(Figure 25)

KANAPOI MATERIAL. 71, frontlet with Rt. and Lt. h/cs.

The sole specimen comprises a frontlet with proximal horn cores that have long pedicels hollowed out by very large basal sinuses. The horn cores diverge outward and taper rapidly upward from their bases. They are ornamented by strong longitudinal ridges and furrows. The face was evi-

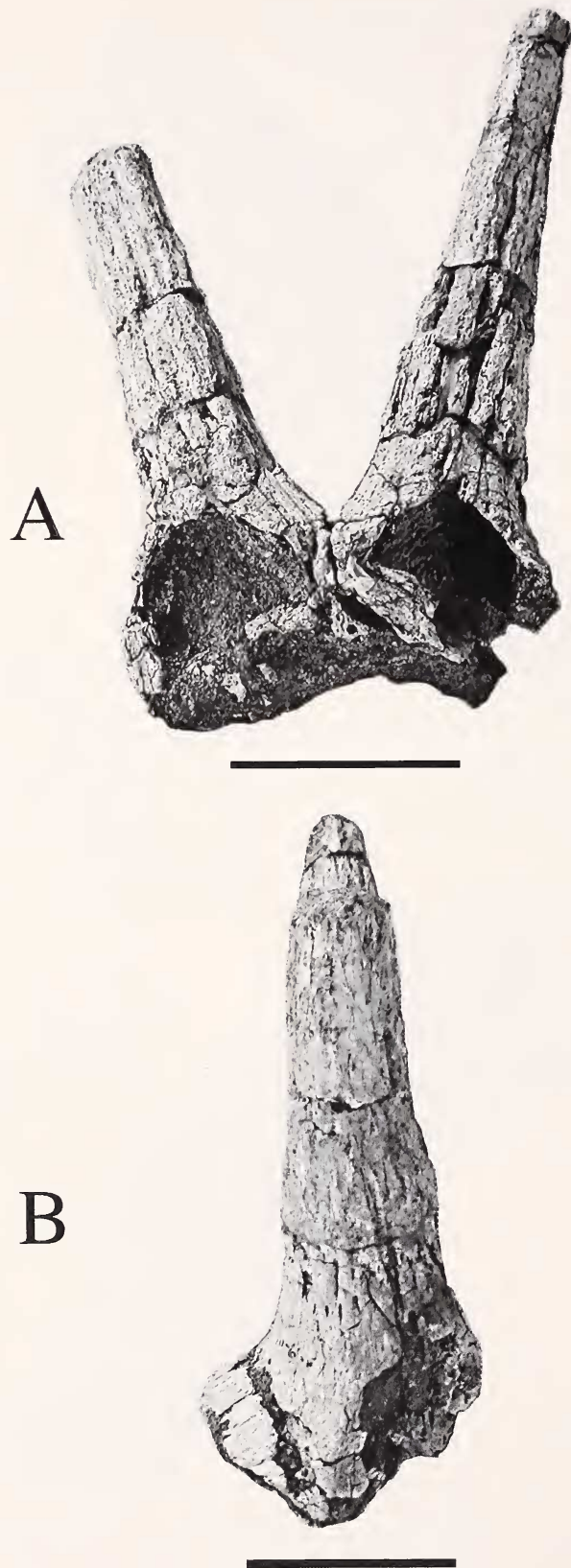


Figure 25 KNM-KP 71, *Damalacra* cf. *D. neanica* frontlet with proximal horn cores; A = anterior view; B = right lateral view; scales = 5 cm

Table 35 Kanapoi Tragelaphini dentition measurements

		109	29273L	29273R	30395	32514
P ⁴	ap					10.3
	tr					14.4
M ¹	ap	23.0	21.2	21.5	18.9	13.8
	tr	16.9	15.9	15.4	23.0	14.2
M ²	ap		21.8	22.8	27.8	18.1
	tr		16.6	17.0	24.0	17.8
M ³	ap					21.7
	tr					16.2
		30396	30441			
M ¹	ap		19.7			
	tr		16.5			
M ²	ap					
	tr					
M ³	ap	26.1				
	tr	14.4				
		66	67	32574	32881	32570
P ₃	ap				11.9	12.9
	tr				7.4	8.0
P ₄	ap					14.4
	tr					8.9
M ₁	ap			17.6		15.9
	tr			10.2		10.8
M ₂	ap	19.0	18.9			
	tr	13.0				
M ₃	ap	29.9				
	tr	12.7				
		32545	32573	30421	36861	
P ₂	ap	10.2				
	tr	5.7				
P ₃	ap				10.6	
	tr				6.0	
P ₄	ap	16.5			11.0	
	tr	8.3			5.8	
M ₁	ap			16.0		
	tr			10.4		
M ₂	ap	20.9	18.9	20.0		
	tr	12.5	12.3	12.2		
M ₃	ap			26.1		
	tr			12.0		

dently strongly angled on the braincase. From the width of the preserved portion of the braincase at the base of the horn cores, this was evidently a much larger animal than *Damalacra* species A or B from Lothagam (Harris, 2003b). The base of the right horn core measures 36 mm (anteroposteriorly) by 33 mm (transversely); the left horn core measures 24 × 33 mm.

This specimen is closer to *D. neanica* than to *D. acalla* Gentry, 1980, by virtue of the uncompressed and widely divergent horn cores, but the horn cores are smaller than male representatives of this species from Langebaanweg.

Table 36 Kanapoi *Simatherium* cf. *S. demissum* horn core measurements

	30612
Lt h/c ap	86
tr	65
Rt. h/c ap	
tr	
lt	290+
Width between h/cs	160

Damalacra sp. A (Figure 26; Table 40)

KANAPOI MATERIAL. 64, proximal Lt. h/c; 26560, proximal Lt. h/c; 29270, Rt. h/c; 30630, distal h/c frags; 30447, proximal Lt. h/c.

This species had a long, slender horn core very reminiscent of specimens attributed to *Damalacra* sp. A from Lothagam (Harris, 2003b). The horn core was mediolaterally compressed with a flattened lateral surface. It tapers gently upward from the base. It is teardrop-shaped in transverse section with a carinate posterior border. The horn cores diverge outward and slightly backward from the

Table 37 Kanapoi *Simatherium* cf. *S. demissum* teeth measurements

		29265L	29265R
P ²	ap	19.18	
	tr	17.47	
P ³	ap	18.52	
	tr	22.37	
P ⁴	ap	16.72	16.88
	tr	22.3	
M ¹	ap	23.1	
	tr	24.73	
M ²	ap	27.86	27.03
	tr	27.43	
M ³	ap	29.98	30.36
	tr	25.77	29.43
		96	
P ₂	ap	14.64	
	tr	9.31	
P ₃	ap	20.19	
	tr	11.61	
P ₄	ap	21.66	
	tr	13.24	
M ₁	ap	21.75	
	tr	17.18	
M ₂	ap	27.97	
	tr	17.71	
M ₃	ap	37.98	
	tr	17.09	



Figure 26 KNM-KP 29270, *Damalacra* sp. A, right horn core; A = lateral view; B = medial view; scale = 5 cm

Table 38 Kanapoi Hippotragini teeth measurements

		32526	483 B-D
P ⁴	ap		11.5
	tr		11.2
M ¹	ap	21.1	19
	tr	23.8	13.7
M ²	ap		20.2
	tr		15.5
M ³	ap		25.1
	tr		15.9
29274			
M ₂	ap	24.91	
	tr	14.41	
M ₃	ap	30.93	
	tr	14.1	

base but recurve to upright in their distal portion. There are faint transverse annulations on the anterior surface and strong longitudinal ridges and furrows on the lateral and medial surfaces.

Damalacra acalla Gentry, 1980

The cranium of *Damalacra acalla* is of similar size and proportions to that of *D. neanica*. The horn

Table 40 Kanapoi *Damalacra* sp. A horn core measurements

		26560	64A	29270	30447
Rt h/c	ap			23.9	
	tr			17.6	
	lt			160+	
Lt h/c	ap	23.8	22.3		21.1
	tr	18.3	17.4		18.1
	lt				

cores are mediolaterally compressed with localized (usually medial) swelling at their bases, sometimes with flattened lateral surface along part of their length, with more definite backward curvature than in *D. neanica* and less marked distal divergence, inserted close behind orbits, and with a more nearly horizontal boundary between the top of the pedicel and the horn core proper. Other differences from *D. neanica* are that the braincase roof is less steeply inclined, more curved in profile, and with a parietal hump that is as well developed as in living *Damaliscus*; the mastoid exposure is large but less expanded especially medioventrally, and the auditory bullae are slightly larger and much more inflated. Female horn cores are smaller than those of the males. The teeth are of similar morphology to *D. neanica* (after Gentry, 1980).

Damalacra cf. *D. acalla* (Figure 27; Table 41)

KANAPOI MATERIAL. 30157, calvaria with Rt. and Lt. h/cs; 32557, proximal Rt. h/c frag; 32876, distal h/c frag.

This alcelaphin is best represented by KP 30157, a calvaria with proximal horn cores that differs from KP 71 by its smaller size and less strongly divergent but more strongly compressed horn cores. The horn cores are inserted close together above the orbits on long pedicels. At their base, they are oval in transverse section. They rise upward but diverge gently outward about halfway up and become more strongly mediolaterally compressed in their distal portion. There is slight anticlockwise torsion in the right horn core when viewed from above. The face is strongly angled on the braincase. There is a large

Table 39 Kanapoi Reduncini tooth measurements

		29275					
P ²	ap						
	tr						
P ³	ap						
	tr						
P ⁴	ap						
	tr						
M ¹	ap	13.8					
	tr	17.6					
M ²	ap	18.1					
	tr	21.8					
M ³	ap	22.1					
	tr						
		75	463	29275	29276	29279	30626
P ₂	ap				8.0	7.7	
	tr				6.9	4.6	
P ₃	ap	10.4			11.7		
	tr	6.9			9.0		
P ₄	ap				14.9		14.1
	tr				9.2		7.8
M ₁	ap	16.1	15.8	16.0	17.3		
	tr	9.6	10.7	11.8	13.0		
M ₂	ap				19.6		
	tr				14.3		
M ₃	ap				31.1		
	tr				14.8		

Table 41 Kanapoi *Damalacra* cf. *D. acalla* horn core measurements

		30157	32557
Rt h/c	ap	33.1	33.9
	tr	25.7	26
	lt		
Lt h/c	ap	34.2	
	tr	24.7	
	lt		

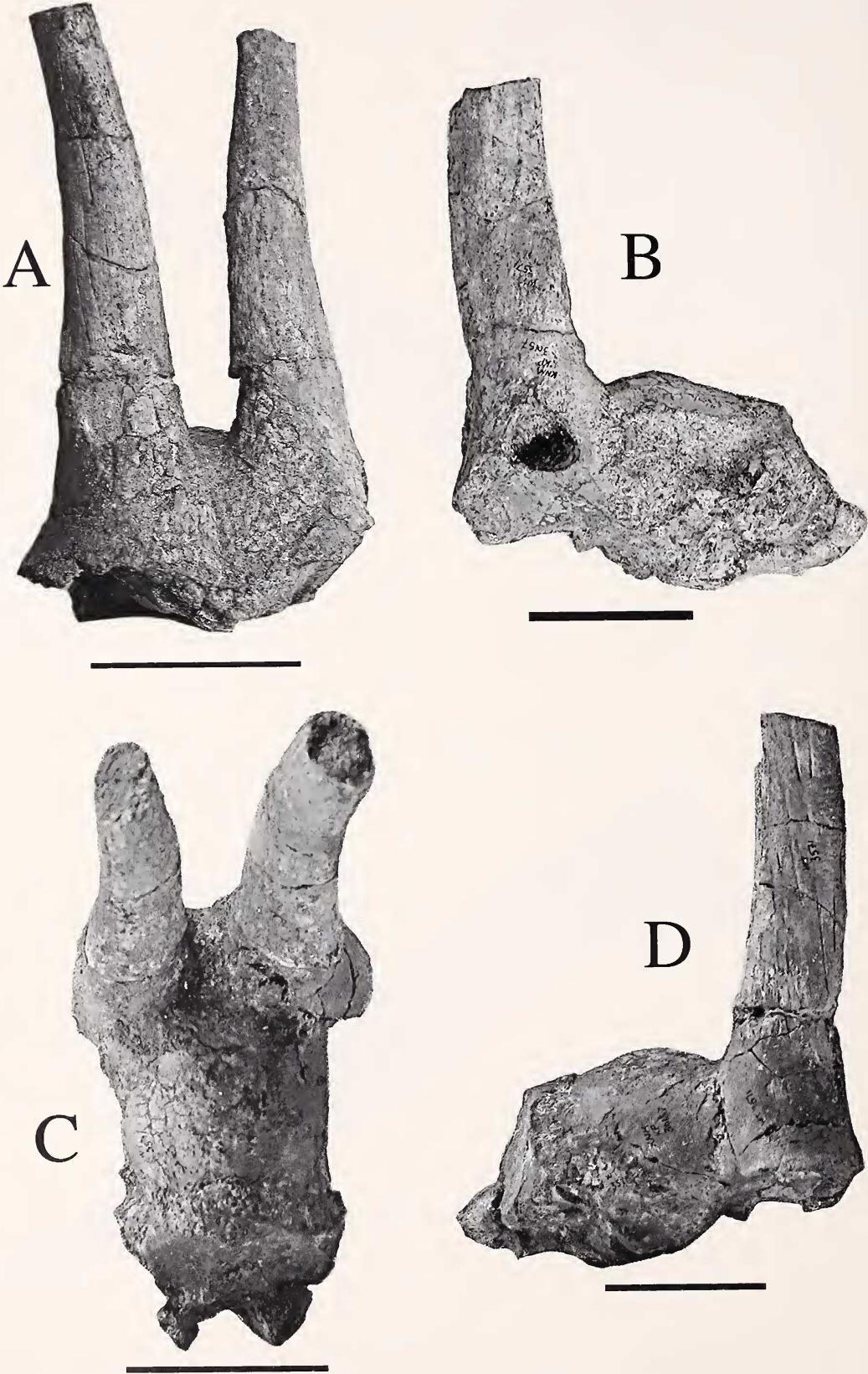


Figure 27 KNM-KP 30157, *Damalacra* cf. *D. acalla*, calvaria with proximal horn cores; A = anterior view; B = left lateral view; C = dorsal view; D = right lateral view; scales = 5 cm

Table 42 Kanapoi Alcelaphini tooth measurements

		493	110	111	83	73	31739
M ¹	ap		19.8			21.5	18.9
	tr		11.9			15.6	12.5
M ²	ap				26.3		
	tr				22.1		
M ³	ap			30.7		26.5	
	tr			17.1		17.4	
dP ₄	ap	22.9					
	tr	8.2					
		387	462	44128			
M ¹	ap			18.5			
	tr			13.3			
M ²	ap		24.8				
	tr		13.5				
M ³	ap	27.3	27.7	24			
	tr	19.3	17	16.8			
		74	108	110	30406	31733	31033 462
P ₂	ap					5.9	
	tr					4.5	
P ₃	ap					11.1	
	tr					6.6	
P ₄	ap					14.9	
	tr					8.2	
M ₁	ap					20.6	17.4
	tr					9.8	9.5
M ₂	ap					25.7	
	tr				10.7	9.8	
M ₃	ap		26.3		27.1		
	tr	11.9	9.9	9.5	10.8	9.7	10.2

"*Parmularius*-like" bulge on the top of the braincase, midway between the horn core bases and the nuchal crest.

The shape of the calvaria and horn cores are close to those of *Damalacra acalla* from Langebaanweg but the horn cores would group in size with the smallest *D. acalla* specimens and the calvaria has a much more pronounced parietal boss.

Alcelaphini gen. indet. (Table 42)

KANAPOI MATERIAL. 73, A = Lt. M¹, B = Rt. M³; 74, Lt. M₃ frag; 83, Rt. M²; 108, Rt. M₃;

110, Rt. M₃ frag and Rt. M/; 111, Lt. M³; 287, Lt. M³; 462, Rt. M², Lt. M³, Rt. M₃ frag, tooth and bone frags; 493, Rt. dP₄; 30406, Lt. mandible frags (M₂₋₃); 31733, Lt. mandible (P₂-M₃); 31739, Lt. M¹; 311033, Rt. M₁; 44128, Lt. M³ and tooth frags.

A few alcelaphin teeth were recovered but none were associated with alcelaphin horn cores.

Tribe Aepycerotini

This tribe is today represented by the single but variable species *Aepyceros melampus* (Lichtenstein, 1812). Aepycerotins may be a sister group of the alcelaphins (Vrba, 1984) but the two groups have different habitat preferences and dental morphology. Lyrate horned impalas were the dominant bovid in the Nawata Formation of Lothagam (*Aepyceros premelampus* Harris, 2003b). A smaller and less lyrate-horned species predominated in the middle Pliocene strata of the Shungura, Nachukui, and Koobi Fora Formations but the extant species had become dominant by the late Pliocene.

Aepyceros Sundevall, 1847

Aepyceros sp. indet.

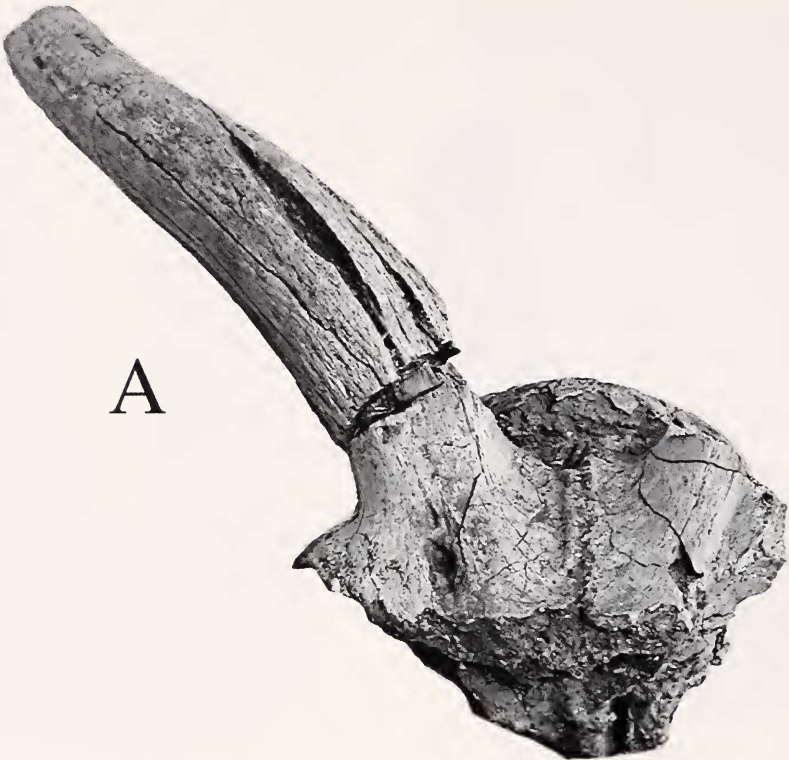
(Figures 28 and 29; Tables 43 and 44)

KANAPOI MATERIAL. 70, prox Rt. h/c; 95, Lt. M²; 99, prox Lt. h/c; 106, Rt. M³; 29259, Rt. mandible (M₁₋₂), Lt. M²⁻³, Rt. M¹⁻²; 29277, calvaria and prox Rt. h/c; 30394, Rt. M; 30417, Lt. M²; 30418, prox Lt. h/c; 30627, Lt. h/c; 30633, h/c frags; 32543, Lt. h/c; 32544, Rt. mandible (P₄-M₁); 32546, Lt. maxilla (P²-M²); 32561, Rt. M²; 32812, Lt. maxilla frag (M¹⁻³); 32823, Rt. M²; 36836, Lt. M¹.

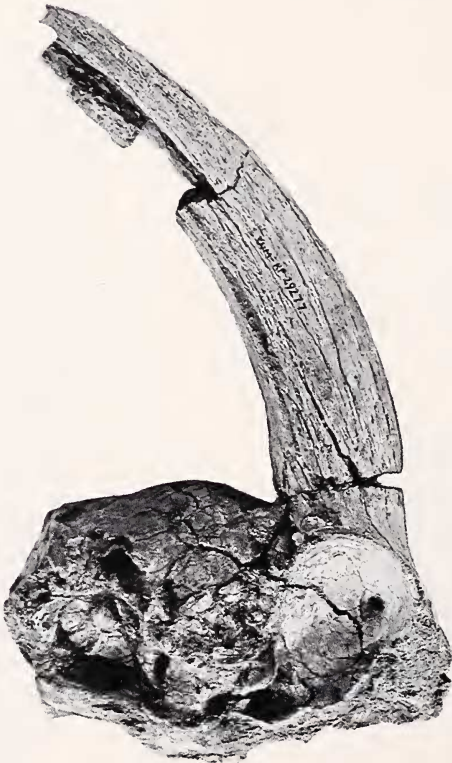
KP 29277 is a rather battered calvaria with the proximal portion of the right horn core but it is sufficiently well preserved to confirm the generic identification. The horn cores are mediolaterally compressed at their base with slight lyrate curvature in anterior view and a gentle sigmoid curvature in lateral view. In this regard, the Kanapoi impala more strongly resembles *A. shungurae* Gentry, 1985, from the northern portion of the Lake Turkana Basin (Gentry, 1985; Harris, 1991b) by the lack of liration than *A. premelampus* Harris, 2003, from the nearby but somewhat older site of Lothagam (Harris, 2003b). The majority of specimens

Table 43 Kanapoi *Aepyceros* sp. indet. horn core measurements

	prox ap (Rt)	prox tr (Rt)	lt (Rt)	prox ap (Lt)	prox tr (Lt)	lt (Lt)
70	42	41				
99				35	30	
29277	37	32				
30418	36	30				
30627				29	23	
32543	33	28				



A



B

Figure 28 KNM-KP 29277, *Aepyceros* sp. indet., calvaria with proximal right horn core; A = anterior view; B = right lateral view; scales = 5 cm

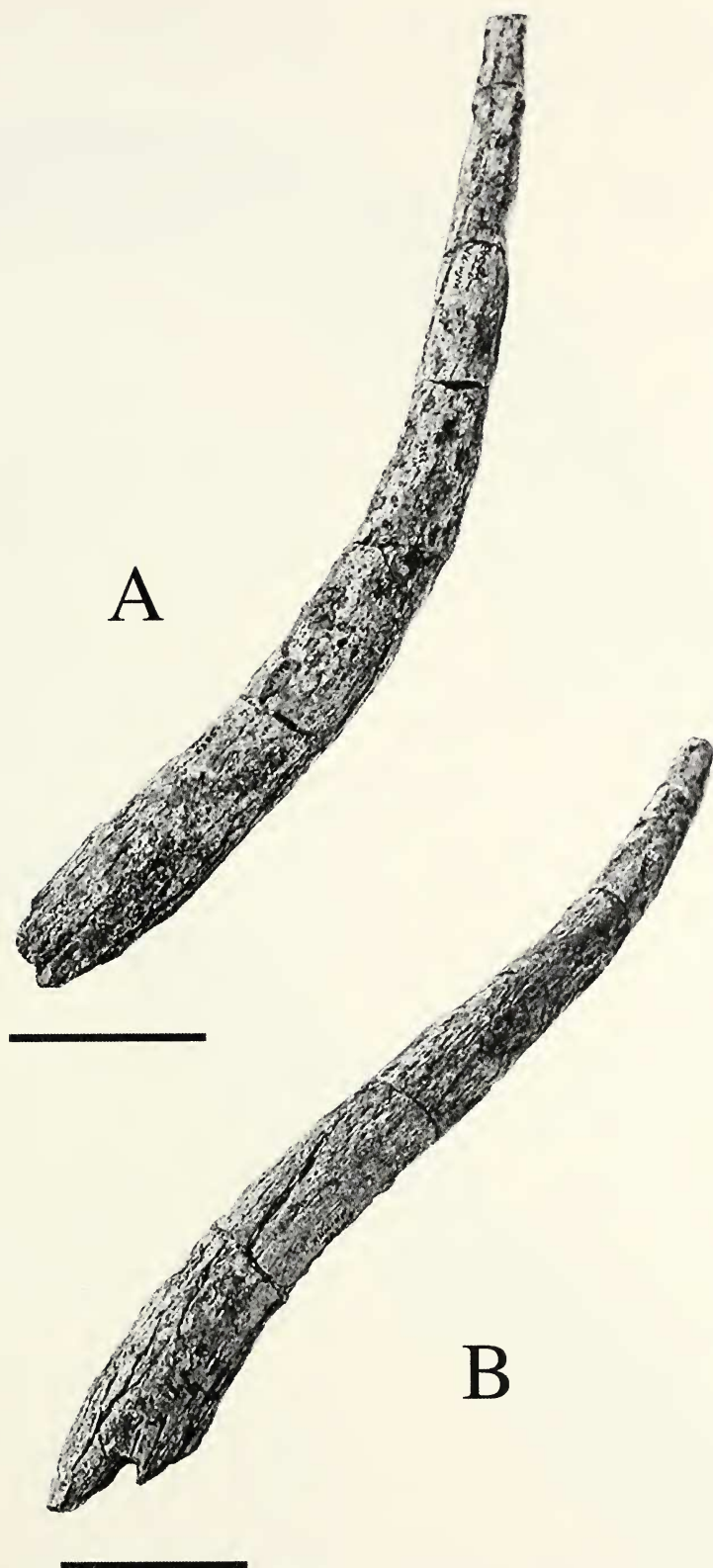


Figure 29 KNM-KP 32543, *Aepyceros* sp. indet. left horn core; A = anterior view; B = lateral view; scales = 5 cm

Table 44 Kanapoi *Aepyceros* sp. indet. teeth measurements

		95	106	29259L	29259R	30417
M ¹	ap				13.5	
	tr				11.1	
M ²	ap	16.6		16.4	16.3	15.3
	tr			13	12.8	11.4
M ³	ap		19.2	18.5		
	tr		11.9	12.3		
		32546	32561	32812	32823	
P ²	ap	7.8				
	tr	7.2				
P ³	ap	7.1				
	tr	8.1				
P ⁴	ap	9.1				
	tr	9.7				
M ¹	ap	11.4				
	tr	12.2				
M ²	ap	15.4	16.5	14.5	17.1	
	tr	12.7	11.6	13.2	12.5	
M ³	ap					
	tr					
		29259R	32544			
P ₄	ap		8.8			
	tr		6.1			
M ₁	ap	12.1	12			
	tr	7.4	8.9			
M ₂	ap	15.1				
	tr	7.9				
M ₃	ap					
	tr					

show slight to moderate transverse annulation; this is most strongly developed in KP 70—the largest specimen whose attribution to *Aepyceros* is slightly less certain than that of the other specimens.

Tribe Antilopini

The Antilopini are small- to medium-sized hypsodont antelopes that appear well adapted to arid areas. The tribe has a long geological history and indeterminate species of gazelles have been reported from the middle Miocene of North (Thomas, 1979) and East Africa (Gentry, 1970).

Gazella de Blainville, 1816

Gazella sp. indet.
(Table 45)

KANAPOI MATERIAL. 29264, Rt. h/c frags; 32513, Lt. and Rt. h/c frags.
Two specimens appear to represent the small and slightly medio-laterally compressed proximal horn cores of an indeterminate species of gazelle.

Table 45 Kanapoi *Gazella* sp. indet. horn core measurements

		29264	32513
Rt h/c	ap	21.5	20.1
	tr	19.3	17.1
Lt h/c	lt		
	ap		19.5
	tr		17.7
	lt		

Tribe Caprini

Caprins, which include domesticated sheep and goats, are documented as common elements of the middle Miocene assemblage from Fort Ternan (Gentry, 1970) but thereafter only appear sporadically in sub-Saharan Africa as rare elements of late Neogene biotas.

Caprini gen. et sp. indet.
(Figure 30)

KANAPOI MATERIAL. 36604, Lt. h/c.

A single, large left horn core with a very pronounced basal sinus may represent an indeterminate species of goat. The horn core is strongly mediolaterally compressed with a flattened lateral surface. It evidently curved backward and outward from the base with a strong lyrate curvature from the anterior view. In some ways, it resembles a large but very flattened impala horn core. At its base, it measures 45.4 mm anteroposteriorly and 31.4 mm transversely.

Tribe Neotragini

Neotragins include about a dozen species of small antelopes that represent the root stock from which the Aegodontia (alcelaphins, antilopins, caprins) emerged (Kingdon, 1982). The tribe is today restricted to Africa. Neotragins representing species of steinbuck and dikdik have been reported from late Miocene assemblages at Lothagam (Harris, 2003b) but their small size tends to make them infrequent components of Pliocene assemblages, although they are known from Langebaanweg (Gentry, 1980) and elsewhere.

Raphiceras H. Smith, 1827

The steenboks (or steinbucks) are moderate-sized neotragins that are distributed discontinuously through open bushland or light woodland in eastern and southern Africa. The horn cores are short to moderately long with little mediolateral compression, inserted widely apart above the back of the orbits, are parallel to one another and, in profile, have a slightly concave anterior edge. Postcornual fossae are present and the supraorbital pits are wide apart (Gentry, 1980).



Figure 30 KNNM-KP 36604, Caprini gen. and sp. indet. left horn core; A = anterior view; B = medial view; scales = 5 cm

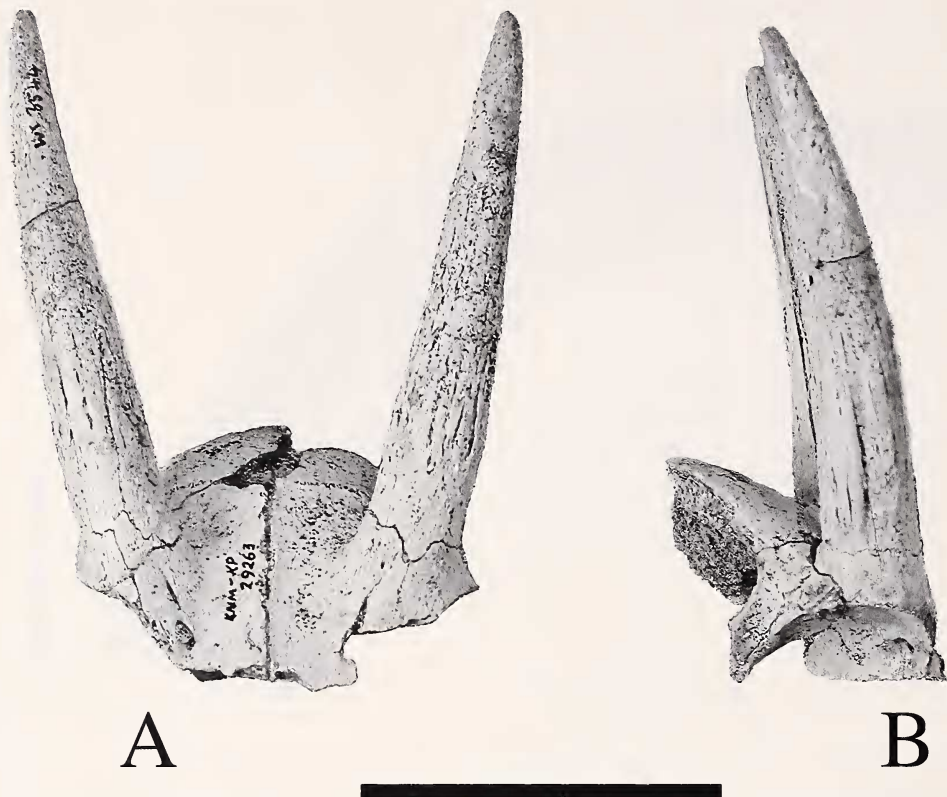


Figure 31 KNM-KP 29263, *Raphiceras* sp. indet. frontlet with horn cores; A = anterior view; B = right lateral view; scale = 5 cm

Table 46 Kanapoi *Raphiceras* sp. indet. measurements

	29263			
Rt h/c ap	14.3			
tr	12.7			
lt	71.6			
Lt. h/c ap	13.7			
tr	14			
lt	66.6			
Width between h/cs	25.2			
	93	30443	36833	30273
P ₂ ap	4.3			
tr	2.8			
P ₃ ap			8.5	
tr			4.5	
P ₄ ap		7.5		
tr		4.8		
M ₁ ap	10.9	9.5		
tr	6.3	6.2		6.3
M ₂ ap	12.0	10.3		10.4
tr	6.6	6.7		7.3
M ₃ ap	17.0	16.3		
tr	5.8	6.4		

Raphiceras sp. indet.
(Figure 31; Table 46)

KANAPOI MATERIAL. 93, Rt. mandible (P₂, M₁₋₃); 29263, frontlet with Lt. and Rt. h/cs; 30273, Lt. M₁₋₃; 30443, Lt. mandible (P₄-M₃); 36833, Rt. mandible frag (P₃₋₄).

A frontlet with right and left horn cores (KP 29263) is a little larger than the equivalent portion of an extant steinbuck cranium but is evidently congeneric. A number of neotragine dentitions that are larger than those of dikdiks are interpreted to represent this genus.

Madoqua Ogilby, 1837

The dikdiks are small, shy antelope that occur singly or in pairs in dry bush country in eastern and southwestern Africa. The horn cores are short, often keeled, compressed anterolaterally to postero-medially, and with some flattening of the postero-medial surface. They are inserted wide apart above the back of the orbits, parallel to one another, and not very upright in lateral view. Postcornual fossa are small and shallow but the supraorbital pits are small and wide apart (Gentry, 1987).

Table 47 Kanapoi *Madoqua* sp. indet. tooth measurements

		103	30207	30416	30427	30537	32547
M ²	ap						
	tr						
M ³	ap	9.3			8.2		
	tr	8.6			7.4		
P ₂	ap						
	tr						
P ₃	ap		4.8				
	tr		3.3				
P ₄	ap		6	6.5			
	tr		4.1	3.7			
M ₁	ap					7.3	
	tr					4.3	
M ₂	ap			7.5	7.2		9.5
	tr			5.1	4.5		5.1
M ₃	ap					10.5	11.1
	tr			4.7		5.1	5.1
		36832	36835	36840	30206A	30206B	
M ²	ap				6.9		
	tr				8.2		
M ³	ap				8		
	tr				7.6		
P ₂	ap						
	tr						
P ₃	ap						
	tr						
P ₄	ap	8.1		7.5			
	tr	3.9		4.2			
M ₁	ap	7.6		7.5	7.3	7.2	
	tr	4.6	4.5	4.6	4.7	4.8	
M ₂	ap		8.9	8.1	8.1		
	tr		5.2	5	5.1	5.2	
M ₃	ap						
	tr						

Madoqua sp. indet.

(Table 47)

KANAPOI MATERIAL. 103, Rt. M³; 30206, Rt. mandible (M₁₋₂), Rt. mandible (M₁₋₂), Lt. M², Rt. M³, humerus frags; 30207, Lt. mandible frag (P₃₋₄), prox scapula, dist Lt. and Rt. humerus; 30416, Rt. mandible frags (P₄, M₂₋₃); 30427, Rt. maxilla frag (M²⁻³); 30537, Lt. mandible (M₁₋₃); 32547, Rt. mandible (M₂₋₃), seven foot bones and distal radius; 36832, Lt. mandible (P₄-M₃); 36835, Rt. mandible (M₁₋₂); 36840, Rt. mandible (P₃-M₂).

Small partial dentitions of comparable size to extant dikdiks represent one of the earliest known species of this genus.

PALEOENVIRONMENTS

Chronologically and stratigraphically, the Kanapoi Formation is equivalent to the lower part of the Nachukui Formation sequence as exposed at Loth-

agam. The lacustrine interval documented in the middle of the Kanapoi sequence represents a southerly extension of the Lonyumun Lake, which at the nearby locality of Lothagam is represented by the Muruogori Member. The terrestrial sediments at Kanapoi may thus be correlated to an upper portion of the Apak Member and the lower portion of the Kaiyumung Member in the Lothagam succession (Feibel, 2003a). More than fifty mammalian species have been recovered from the Kanapoi Formation (Table 48). The percentage distribution of the larger herbivore families in the Kanapoi biota is broadly comparable with that seen in the Apak Member although the represented taxa suggest a slightly younger age for the Kanapoi assemblage and at Kanapoi large suids seem to have replaced part of the bovid population that dominated at Apak (Table 49).

The Nawata Formation sequence at Lothagam documents the interval of time in which C₄ plants (and particularly grasses) underwent a major expansion in Africa, Asia, and North and South America (Cerling et al., 1997). As documented by Cerling et al. (2003a:fig. 12.5), the $\delta^{13}\text{C}$ composition of tooth enamel of mammals with a pure C₄ diet ranges from 1–3 permil whereas that of mammals with a pure C₃ diet in open habitats ranges from –12 to –16 permil. Preliminary results of isotopic analysis of mammalian herbivores from Kanapoi are mostly consistent with the younger radiometric age determinations for the Kanapoi Formation (Table 50). As expected, the elephantoid proboscideans (*Anancus kenyensis*, *Loxodonta adaurora*, *Elephas ekorensis*) all had a C₄ grazing diet, as did the suids *Nyanzachoerus pattersoni* and *Notochoerus jaegeri* and the equid *Eurygnathohippus* sp. All these species had assumed a grazing diet before or during the accumulation of the Apak Member at Lothagam. In contrast, C₃ browse was a major component of the diet of deinotheres (*Deinotherium bozasi*), sivatheres (*Sivatherium* cf. *S. bendeyi*), impalas (*Aepyceros* sp.), and ostriches (*Struthio* sp.). The sole rhino tooth analyzed also indicated a browsing diet. The $\delta^{13}\text{C}$ content of the fossil ostrich eggshell is more negative than those of extant ostriches from Kanapoi and the $\delta^{18}\text{O}$ is more positive; it would appear that there was a greater proportion of C₃ vegetation in the Pliocene ostrich diet compared with that of modern ostriches on the west side of Lake Turkana. Hence, the Lake Turkana Basin in the vicinity of Kanapoi evidently supported a variety of vegetation types and habitats during the early Pliocene. The very positive $\delta^{18}\text{O}$ values for the analyzed rhino and sivathere teeth (Table 50) suggests these animals were obtaining most of their water from the plants that they ate.

Wynn (2000) recognized seven types of paleosols at Kanapoi, all of which provide information about the local ecosystem during the process of soil formation.

Table 48 Kanapoi mammalian faunal list

Taxon	Sample size	Body weight	Locomotion	Diet
Chiroptera				
<i>Hipposideros</i> spp.		A	Ac	I
Insectivora				
<i>Myosorex</i> sp.		A	SA	I
Macroscelidae				
<i>Elephantulus</i> sp.		A	SA	I
Lagomorpha				
Leporidae gen. and sp. indet.		C	T	Hg
Rodentia				
<i>Tatera</i> sp.		A	SA	Hb
Murini gen. indet.		A	SA	Hb
<i>Xerus</i> sp.		B	T	HF
cf. <i>Steatomys</i> sp.		A	T	Hb
Carnivora				
<i>Enhydriodon ekecaman</i>	1	D	Aq	C
cf. <i>Torolutra</i> sp.	1	C	Aq	C
<i>Parabyaena howelli</i>	31	E	T	C
<i>Dinofelis petheri</i>	3	D	T-S	C
<i>Homotherium</i> sp.	4	E	T-S	C
<i>Felis</i> sp.	1	C	T-S	C
<i>Helogale</i> sp.	2	B	T	C
<i>Genetta</i> sp. nov.	3	C	T	C
Primates				
<i>Australopithecus anamensis</i>	59	D/E	TA	O
cf. <i>Galago</i> sp. indet.	1	B	A	O
cf. <i>Ceropithecoides</i> sp. indet.	6	C	TA	HF
Colobinae sp. A	8	D	TA	HF
Colobinae sp. B	1	D	TA	HF
<i>Parapapio ado</i>	50	D	TA	HF
cf. <i>Theropithecus</i> sp.	1	D	TA	HF
Proboscidea				
<i>Deinotherium bozasi</i>	5	H	T	Hb
<i>Anancus kenyensis</i>	2	H	T	Hg
<i>Elephas ekorensis</i>	25	H	T	Hg
<i>Loxodonta adaurora</i>	26	H	T	Hg
<i>Loxodonta exoptata</i>	1	H	T	Hg
Perissodactyla				
<i>Ceratotherium praecox</i>	11	H	T	Hg
<i>Diceros bicornis</i>	4	H	T	Hb
<i>Eurygnathobippus</i> sp. indet.	34	F	T	Hg
Artiodactyla				
<i>Hexaprotodon protamphibius</i>	60	H	Aq	BG
<i>Hexaprotodon</i> sp.	1	H	Aq	BG
<i>Nyanzachoerus pattersoni</i>	77	F	T	Hg
<i>Notochoerus jaegeri</i>	29	F	T	Hg
<i>Notochoerus</i> cf. <i>N. euilus</i>	1	F	T	Hg
<i>Giraffa stillei</i>	5	G	T	Hb
<i>Giraffa jumae</i>	1	H	T	Hb
<i>Giraffa</i> sp. indet.	9	G	T	Hb
<i>Sivatherium</i> cf. <i>S. hendeyi</i>	3	G	T	Hb
<i>Tragelaphus kyaloae</i>	33	F	T	BG

Table 48 Continued

Taxon	Sample size	Body weight	Locomotion	Diet
Tragelaphini gen. indet.	17	F	T	BG
<i>Simatherium</i> cf. <i>S. demissum</i>	4	H	T	Hg
Hippotragini gen. indet.	4	G	T	BG
<i>Kobus</i> sp.	2	F	T	Hg
Reduncini gen. indet.	6	F	T	Hg
<i>Damalacra</i> cf. <i>D. neanica</i>	1	F	T	Hg
<i>Damalacra</i> sp. A	5	E	T	Hg
<i>Damalacra</i> cf. <i>D. acalla</i>	3	F	T	Hg
Alcelaphini gen. indet.	14	F	T	Hg
<i>Aepyceros</i> sp.	18	F	T	Hb
<i>Gazella</i> sp.	2	D	T	Hg
Caprini gen. and sp. indet.	1	E	T	Hg
<i>Raphiceras</i> sp.	5	D	T	Hb
<i>Madoqua</i> sp.	10	C	T	Hb

Ecovvariable categories

Code	Body weight	Code	Locomotor patterns	Code	Feeding preferences
A	0–100 g	T	Terrestrial	I	Insectivore
B	100–1,000 g	TA	Terrestrial–arboreal	F	Frugivore
C	1–10 kg	SA	Semiarboreal	HF	Herbivore–frugivore
D	10–45 kg	A	Arboreal	Hb	Brower
E	45–90 kg	S	Scansorial	Hg	Grazer
F	90–180 kg	TS	Terrestrial–scansorial	BG	Brower–grazer
G	180–360 kg	Aq	Aquatic	C	Carnivore
H	360+ kg	Ae	Aerial	CI	Carnivore–insectivore
		F	Fossorial	O	Omnivore
		TF	Terrestrial–fossorial		

1. Modern analogues of the Aberegaiya paleosols are found throughout semiarid regions of East Africa on floodplains flanking large river systems and support edaphic savanna grasslands within low tree–shrub savanna mosaics.
2. The Lorenyan paleosol is found in delta deposits where it represents brief emergence of the delta flats and desiccation of the clayey parent material; modern analogues occur on the Omo River Delta at the north end of Lake Turkana where they support sparsely vegetated grasslands with variable admixtures of ephemeral forbs.
3. Dite paleosols, from which most of the hominid fossils were derived, were better drained but formed in broadly similar conditions to the Aberegaiya and Lorenyang paleosols. Modern analogues to the Dite paleosols are found in the lower Omo Valley, where well-drained soils support low tree–shrub savanna vegetation in semi-arid to arid climatic regimes.
4. Abilat paleosols are calcic xerosols. Their characteristics are intermediate between Dite and Aberegaiya paleosols and they are believed to represent transitional habitats between these two pedotypes. Vegetation growing on Abilat soils would thus have been transitional between the forb-dominated edaphic grasslands of the

Aberegaiya pedotype and the low tree–shrub savanna of the Dite pedotype.

5. The Nasua paleosol is found on delta sediments. Like the Lorenyang, the Nasua paleosol represents brief emergence of the delta flats but supported denser vegetation; similar modern clayey soils are found on the Omo Delta, where they support shrub thickets of aquatically adapted *Acacia* and *Cadaba* species.
6. Kabisa paleosols with vertical rhizoliths are found in channel sandstones in the upper fluvial series; modern counterparts in the lower Turkana Basin occur in the sandy soils of ephemeral channels, where they support gallery woodland and thicket vegetation—often dominated by *Acacia tortilis*.
7. Akai–Ititi paleosols have horizontal rhizoliths representing root mats in nearshore environments where groundwater is shallow; modern analogues fringe the Omo Delta and support lakeside and streamside grasslands with root mats of *Phragmites*, *Typha*, and *Cyperus* species and *Loudetia phragmatoides* or *Sporobolus spicatus*.

Wynn's (2000) overall interpretation of the prevailing habitats at Kanapoi was that they strongly resembled habitats that presently occur in the re-

Table 49 Percentage distribution of large herbivores at Lothagam and Kanapoi

	Lr Nawata	Ur Nawata	Apak	Kanapoi	Kaiyumung
Elephantoidea	4.73	1.97	11.26	13.95	1.52
Rhinocerotidae	4.73	5.90	5.30	4.26	6.06
Equidae	10.11	11.52	8.61	8.04	13.64
Hippopotamidae	20.65	18.54	12.58	14.42	0.00
Suidae	24.52	18.82	13.25	25.06	36.36
Giraffidae	2.80	2.53	5.96	4.26	4.55
Bovidae	32.47	40.73	43.05	30.02	37.88
	100.00	100.00	100.00	100.01	100.00

Table 50 Results of stable isotope analysis of Kanapoi herbivores

	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
<i>Struthio</i> sp.		
WT 3597	-8.66	10.89
<i>Anancus kenyensis</i>		
KP 30442	-0.13	-1.11
<i>Elephas ekorensis</i>		
KP 30173	-1.74	-1.32
WT 3570	-1.48	2.37
<i>Loxodonta adaurora</i>		
KP 390	-2.73	0.87
30196	-2.5	1.05
30196	-2.34	1.09
30596	-1.08	2.2
KP 383	-2.99	-0.36
<i>Deinotherium bozasi</i>		
WT 3617	-12.43	-1.75
Rhinocerotidae gen. indet		
WT 3223	-9.98	4.71
<i>Eurygnathohippus</i> sp.		
30233	1.24	2.09
<i>Nyanzachoerus pattersoni</i>		
KP 205	-6.5	1.19
WT 3222 (M ₃)	-1.94	1.14
KP-X10	-1.19	-0.22
<i>Notochoerus jaegeri</i>		
KNM-3348 B	-1.74	1.43
KP 241	-2.01	1.07
KP 265	-5.47	-2.19
WT 3227	-1.74	1.78
<i>Sivatherium</i> cf. <i>S. hendeyi</i>		
KP 30227	-9	8.6
<i>Aepyceros</i> sp.		
WT 3240-Aepy	-10.02	1.36
WT 3240	-9.77	1.46

gion of the modern Omo River Delta at the north end of Lake Turkana. Most of the hominids derive from Dite paleosols that he interpreted to have supported low tree-shrub savanna vegetation in a semiarid climate with an annual rainfall that ranged from 350 to 600 mm. Wynn (2000) suggested that Kanapoi may represent the earliest known occurrence of hominids venturing into relatively open habitats. However, Ward et al. (1999) caution that many of the hominid specimens show evidence of carnivore damage. Thus, it is possible that the hominid remains were transported by carnivores to the locations where they accumulated. Other paleosols ranged from poorly drained Vertisols with forb-dominated edaphic grassland in local shallow depressions to well-drained alluvial soils supporting gallery woodland adjacent to stream courses. The proportion of soil carbonate contributed by C₄ plants (i.e., grasses) ranges from 25% in the Kabisa paleosol to 40% in the Dite and Abilal paleosols (Wynn 2000).

Confirmation of the nature of the terrestrial habitats during the interval that the early Pliocene assemblage accumulated at Kanapoi is provided by the dietary adaptations of the terrestrial vertebrate fossils (Table 48). Proboscideans amount to about 14% of the large vertebrate biota: *Loxodonta adaurora* and *Elephas ekorensis* predominate, whereas *Anancus* and *Deinotherium* are only sparsely represented. Elephantids and gomphotheres had acquired a grazing diet by the beginning of the Pliocene and their presence at Kanapoi appears to signify open habitat in the near vicinity of the Kanapoi Delta, although the presence of *Deinotherium* confirms an ample supply of C₃ vegetation. Rhinos were represented by the predecessors of the two extant African species, both of which had acquired their different (grazing versus browsing) dietary specializations by the beginning of the Pliocene. Equids are represented by *Eurygnathohippus*, a grazing hipparionine. Large suids are represented by *Nyanzachoerus pattersoni* and *Notochoerus jaegeri*; both were interpreted as closed habitat species by Bishop (1994) on the basis of their postcranial anatomy but both species were evidently specialized grazers on the basis of the isotopic composition of their tooth

Table 51 Stratigraphic distribution of bovid tribes at Lothagam and Kanapoi

	Lr Nawata	Ur Nawata	Apak	Kanapoi	Kaiyumung
Tragelaphini	3.33	2.08	20.63	39.37	16.00
Bovini	1.33	2.08	9.52	3.15	28.00
Boselaphini	24.67	7.64	3.17		
Hippotragini	5.33	5.56	4.76	3.94	
Reduncini	11.33	21.53	9.52	7.09	8.00
Alcelaphini	4.67	17.36	14.29	18.11	12.00
Aepycerotini	48.00	40.28	31.75	14.17	36.00
Antilopini	0.67	1.39	4.76	2.36	
Neotragini	0.67	2.08	1.59	11.81	
	100.00	100.00	100.00	100.00	100.00

enamel (Harris and Cerling, 2002; Cerling et al., 2003b). Giraffids were relatively uncommon constituents of the Kanapoi assemblage but both sivatheres and giraffines were C_3 browsers at that point in time. Bovids, as usual, are the most commonly encountered terrestrial herbivores. Tragelaphins, aepycerotins, and neotragins—now all closed habitat or forest-edge forms—make up two thirds of the Kanapoi bovid assemblage, but the presence of bovins, reduncins, hippotragins, and

alcelaphins is indicative of nearby sources of grass. In contrast with the bovid assemblages from the Apak and Kaiyumung Members, the Kanapoi bovid assemblage has more tragelaphins and alcelaphins but fewer bovins and aepycerotins—which may be interpreted to represent drier and less wooded habitats in the vicinity of Kanapoi (Table 51). Overall, grazing species outnumber browsing species by a ratio of nearly two to one; in terms of numbers of individuals, browsers out-

Frugivores versus Non-arboreal

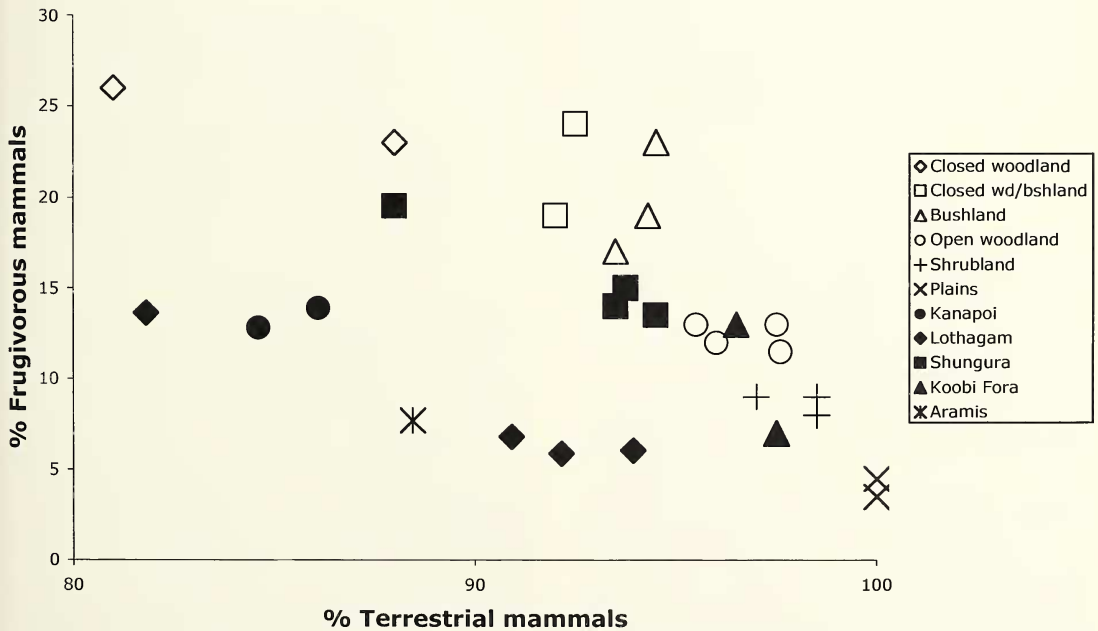


Figure 32 Graph depicting ecological structural analysis of frugivorous mammals and nonarboreal mammals from modern African habitats and from Pliocene assemblages from the Lake Turkana Basin. Data for extant habitats and assemblages from the Shungura and Koobi Fora Formations are from Reed (1997); those for Lothagam assemblages are from Leakey and Harris (2003); those for Aramis are from WoldeGabriel et al. (1994). Of the two data points representing Kanapoi, that on the right is for the assemblage from below the lacustrine interval, that on the left is for the assemblage from above the lacustrine interval

Fresh Grass Grazers versus Terrestrial

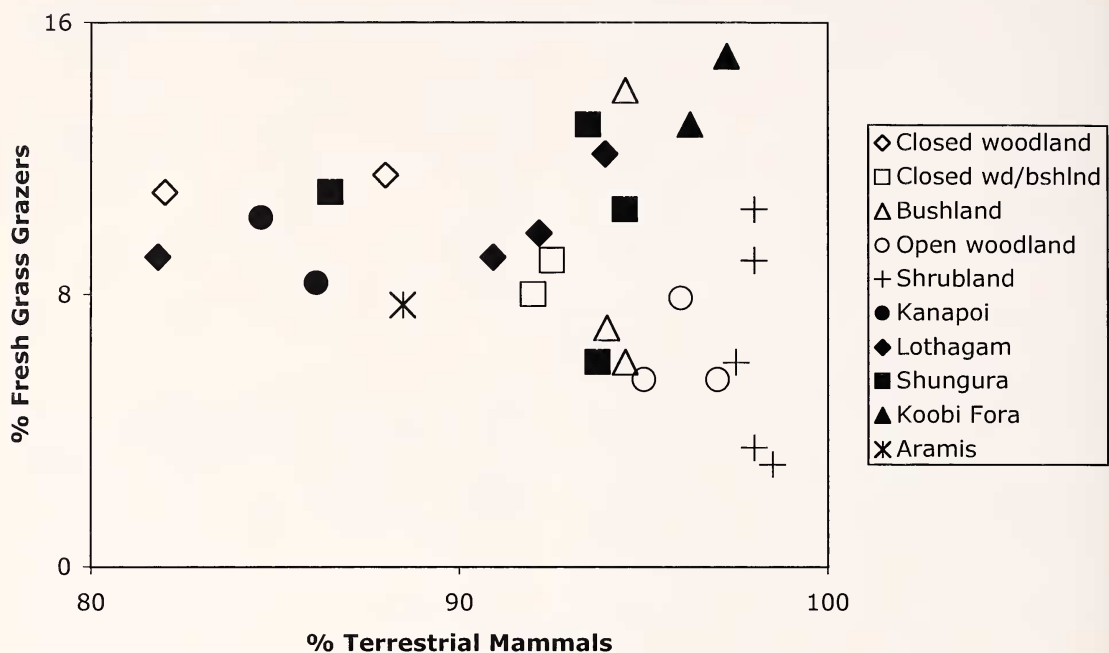


Figure 33 Graph depicting ecological structural analysis of fresh grass grazing mammals and terrestrial mammals from modern African habitats and from Pliocene assemblages from the Lake Turkana Basin. Data points as for Figure 32

number grazers by three to one. In confirmation, the Kanapoi small mammals suggest a relatively dry climate and open habitat (Appendix).

The Kanapoi large-mammal assemblage shares many elements with that from the 4.4 Ma site of Aramis, Ethiopia (WoldeGabriel et al., 1994), although, with the exception of the primates, most of the Aramis fossil material has yet to be described in detail. Taxa shared by Kanapoi and Aramis include elephantids (unidentified at Aramis), *Anancus*, *Deinotherium*, *Ceratotherium* cf. *C. praecox*, "*Hipparion*" sp., *Hexaprotodon* sp., *Nyanzachoerus pattersoni*, *Notochoerus jaegeri*, a large and small species of *Giraffa*, and tragelaphins, bovins, and neotragins. However, with the exception of an unidentified kudu (*Tragelaphus* sp.), large vertebrates are rare at Aramis, as are aquatic vertebrates. WoldeGabriel et al. (1994) interpret the dominance of colobines and kudus at Aramis to be a strong indication of a closed, wooded environment. However, the presence at an early Pliocene site of elephantids, *Anancus*, *Ceratotherium*, an equid, a hippo, *Nyanzachoerus*, *Notochoerus*, and bovins is indicative of a diverse open-country grazing component in the biota. Moreover, the larger genera of early Pliocene colobines were more terrestrial than their extant counterparts (Leakey et al., 2003) and hence the dominance of colobines may not necessarily mandate the presence of closed woodland. As at Aramis, tragelaphins were the

most abundant bovids recovered from Kanapoi. However, in contrast with the situation at Aramis, papionin primates far outnumbered the colobines. On balance, Kanapoi would appear to represent habitats that were similar to but more open than those of Aramis. Andrews and Humphrey (1999) stated that the fossil assemblages from both Aramis and Kanapoi are underrepresented by small mammals that often provide a more precise assessment of the prevailing paleoenvironments than do large migratory species. Large quantities of micromammals that were retrieved by the National Museums of Kenya expeditions have yet to be studied in detail (see Appendix) and the bulk of the nonprimate component of the Aramis fauna has also yet to be studied in depth.

Ecological diversity provides a different means from taxonomic uniformitarianism for analyzing the community structure of fossil mammalian faunas in order to obtain information about the habitats represented by faunal assemblages (Andrews et al., 1979). Using this methodology, Andrews and Humphrey (1999) interpret the Kanapoi material collected by American expeditions in the 1960s, as "... dominated by medium- to large-sized terrestrial species and both browsers and grazers are well represented. The high terrestrial component in the fauna places it with the drier end of the present-day woodland and bushland ecosystems suggesting open woodland with abundant grass."

Ecological structural analysis as formulated by Reed (1997) provides a different interpretation. Reed established that habitats were predicted by locomotory adaptations and characterized by trophic ecovariates and found that it was possible to differentiate between different terrestrial habitats by plotting the percentage of frugivorous mammals against the percentage of nonarboreal mammals (Reed, 1997:fig. 5A). Similar results were obtained by plotting the percentage of fresh grass grazers against percentage of terrestrial mammals and this also established the presence/absence of edaphic grassland (Reed, 1997:fig. 5B). The estimated body weights, locomotor adaptations, and feeding preferences for the Kanapoi mammals are listed in Table 48. When Pliocene assemblages from the Lake Turkana Basin are superimposed on the modern habitat plots for frugivores versus nonarboreal mammals (Fig. 32), the two Kanapoi assemblages (above and below the Lonyumun Lake incursion) plot with the closed woodland assemblages. A similar grouping occurs when the Kanapoi assemblages are superimposed on the graph of fresh grass grazers versus terrestrial mammals (Fig. 33). In both cases, the Kanapoi assemblages plot close to those from the Kaiyumung Member at Lothagam and Shungura Member B in the lower Omo Valley. The reason why the Kanapoi assemblages appear to indicate closed woodland is because the primates have been interpreted as at least partly arboreal (requiring shelter in trees at night). Attribution of terrestrial adaptation to one or more of the primate species would skew the sample toward an interpretation of more open habitat. Given that the hominin was bipedal and that early Pliocene cercopithecoids were more terrestrial than later forms, such an interpretation would be more in keeping with the dietary adaptations of the fossil species and the ecological adaptations of their modern counterparts.

SUMMARY

The early Pliocene site of Kanapoi, southwest of Lake Turkana in northern Kenya, has yielded the oldest australopithecines from eastern Africa although a similar age has recently been claimed for a new australopithecine locality in southern Africa (Partridge et al., 2003). Associated with the hominin remains from Kanapoi is a diverse vertebrate fauna that has been recovered from fluvial and lacustrine sediments dating between 4.17 and 4.07 Ma. The Kanapoi tetrapod fauna is much more prolific than that from any other similarly aged locality elsewhere in the Lake Turkana Basin (Nachukui and Koobi Fora Formations). The assemblage includes 24 species of fish, 7 species of chelonians, 4 species each of crocodylians and birds, and over 50 species of mammals. Few of the recognized species are new but micromammals have not yet been thoroughly investigated. Relatively complete suid specimens mandate the transfer of the species

Nyanzachoerus jaegeri to the genus *Notochoerus*. Paleosols associated with the fauna remains suggest a mixture of open and closed habitats similar to those currently found in the vicinity of the Omo Delta at the north end of Lake Turkana. Such an interpretation is supported by the dietary adaptations of the herbivorous fossil mammals and the habitats exploited by their living representatives.

ACKNOWLEDGMENTS

We thank the Government of Kenya and the Trustees of the National Museums of Kenya for permission to study the Kanapoi fossils and the directors of the National Museums of Kenya and Natural History Museum of Los Angeles County for logistical support that helped expedite this manuscript. Fieldwork at Kanapoi was funded by the National Geographic Society and National Science Foundation (SBR 9601025) and made possible by donations of fuel by Caltex (Kenya) and the loan of light aircraft belonging to Jonathan and Richard Leakey. We thank also the preparation and curatorial staff of the Division of Palaeontology at the National Museums of Kenya, Nairobi, and the many people who participated in the 1994–97 field expeditions and whose names are acknowledged in Ward et al. (2001). We gratefully acknowledge helpful discussions with Craig Feibel, Nina Jablonski, Kathy Stewart, Lars Werdelin, and Alisa Winkler, and we thank Hank Wesselman for his observations on the Kanapoi micromammals, Diana Mattheissen for her notes on the Kanapoi birds, and Anthony Macharia for his help with the GIS database. Isotopic analyses were undertaken in the Geochemistry and SIRFER Laboratories of the University of Utah and were underwritten by support from NSF and the Packard Foundation. Drs. Nina Jablonski and Tim White, an anonymous referee, and members of the Scientific Publications Committee for the Natural History Museum of Los Angeles County, who kindly offered suggestions that helped improve the manuscript.

LITERATURE CITED

- Andrews, P. J., and L. Humphrey. 1999. African Miocene environments and the transition to early hominines. In *African biogeography, climate change, and human evolution*, eds. T. Bromage and F. Schrenk, 282–300. Oxford: Oxford University Press.
- Andrews, P. J., J. M. Lord, and E. M. Nesbit Evans. 1979. Patterns of ecological diversity in fossil and modern mammalian faunas. *Biological Journal of the Linnean Society* 11:177–205.
- Arambourg, C. 1934. Le *Dinotherium* des Gisements de l'Omo. *Comptes Rendues de la Société géologique de France* 1934:86–87.
- . 1944. Les hippopotames fossiles d'Afrique. *Compte Rendu de l'Académie des Sciences* 218:602–604.
- . 1959. Vertébrés continentaux du Miocène supérieure de l'Afrique du Nord. *Publ. Service de la Carte. Géologique d'Algérie (Alger), Nouvelle Series, Paléontologie Mémoires* 4:1–161.
- Beden, M. 1987. Fossil Elephantidae from Laetoli. In *Laetoli: A Pliocene site in northern Tanzania*, eds. M. D. Leakey and J. M. Harris, 259–293. New York: Oxford University Press.
- Bernor, R. L., and J. M. Harris. 2003. Systematics and evolutionary biology of the Late Miocene and Early Pliocene Hipparionine equids from Lothagam, Ken-

- ya. In *Lothagam: The dawn of humanity in eastern Africa*, eds. M. G. Leakey and J. M. Harris, 387–438. New York: Columbia University Press.
- Bishop, L. C. 1994. Pigs and the ancestors: Hominids, suids, and environments during the Plio-Pleistocene of East Africa. Ph.D. dissertation, Yale University.
- Boisserie, J.-R. 2002. Nouveaux Hippopotamidae du Tchad et Ethiopie: Implications phylogénétiques et paléoenvironnementales. Ph.D. dissertation, Université de Poitiers.
- Broom, R. 1925. On evidence of a giant pig from the Late Tertiaries of South Africa. *Records of the Albany Museum* 3:307–308.
- Cerling, T. E., J. M. Harris, and M. G. Leakey. 2003a. Isotope ecology of the Lothagam sequence. In *Lothagam: The dawn of humanity in Africa*, eds. M. G. Leakey and J. M. Harris, 605–624. New York: Columbia University Press.
- . In press. Environmentally driven dietary adaptations in African mammals. In *History of atmospheric CO₂ and the impacts on plants, animals, and ecosystems*, eds. J. R. Ehleringer, M. D. Dearing, and T. E. Cerling. New York: Springer-Verlag.
- Cerling, T. E., J. M. Harris, M. G. Leakey, and N. Mudida. 2003b. Isotopic ecology of the Lake Turkana Basin. In *Lothagam: the dawn of humanity in Africa*, eds. M. G. Leakey and J. M. Harris, 583–603. New York: Columbia University Press.
- Cerling, T. E., J. M. Harris, B. J. MacFadden, M. G. Leakey, J. Quade, V. Eisenmann, and J. R. Ehleringer. 1997. Global vegetation change through the Miocene/Pliocene boundary. *Nature* 389:153–158.
- Churcher, C. S. 1978. Giraffidae. In *Evolution of African mammals*, eds. V. J. Maglio and H. B. S. Cooke, 509–535. Cambridge: Harvard University Press.
- . 1979. The large paleotragine giraffid (*Palaeotragus germaini*) from the Late Miocene of Lothagam Hill. *Breviora* 453:1–8.
- Coe, M. 1972. Ecological studies of the small mammals of South Turkana. *Geographical Journal* 138:316–338.
- Cooke, H. B. S., and R. F. Ewer. 1972. Fossil Suidae from Kanapoi and Lothagam, Kenya. *Bulletin of the Museum of Comparative Zoology Harvard* 143(3):149–295.
- Cooke, H. B. S., and Q. B. Hendey. 1992. *Nyanzachoerus* (Mammalia: Suidae: Tetraodontinae) from Langebaanweg, South Africa. *Durban Museum Novitates* 17:1–20.
- Coppens, Y. 1971. Une nouvelle espèce de Suidé du Villafranchien du Tunisie, *Nyanzachoerus jaegeri* nov. sp. *Comptes Rendus Hebdomadaires des Séances, Académie des Sciences (Paris)* 272:3264–3267.
- Coppens, Y., V. J. Maglio, C. T. Madden, and M. Beden. 1978. Proboscidea. In *Evolution of African mammals*, eds. V. J. Maglio and H. B. S. Cooke, 333–367. Cambridge: Harvard University Press.
- Coryndon, S. C. 1977. The taxonomy and nomenclature of the Hippopotamidae (Mammalia, Artiodactyla) and a description of two new fossil species. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B80*(2):61–88.
- Dietrich, W. O. (1942). Altestquartäre Säugetiere aus den südlichen Serengeti, Deutsch Ost-afrika. *Paleontographica* 94:43–133.
- Feibel, C. S. 2003a. A Stratigraphy and depositional history of the Lothagam sequence. In *Lothagam: The dawn of humanity in eastern Africa*, eds. M. G. Leakey and J. M. Harris, 17–30. New York: Columbia University Press.
- . 2003b. Stratigraphy and depositional setting of the Pliocene Kanapoi Formation, Lower Kerio Valley, Kenya. In *Geology and vertebrate paleontology of the Early Pliocene site of Kanapoi, northern Kenya*. Edited by J. M. Harris and M. G. Leakey. *Contributions in Science* 498:9–20.
- Fourtau, R. 1920. *Contribution à l'étude de vertébrés Miocènes de l'Égypte*. Cairo: Geological Survey of Egypt, Ministry of Finance. 121 pp.
- Frost, S. R. 2001. New early Pliocene Cercopithecidae (Mammalia: Primates) from Aramis, Middle Awash Valley, Ethiopia. *American Museum Novitates* 3350: 1–36.
- Frost, S. R., and E. Delson. 2002. Fossil Cercopithecidae from the Hadar Formation and surrounding areas of the Afar Depression Ethiopia. *Journal of Human Evolution* 43:687–748.
- Gentry, A. W. 1970. The Bovidae of the Fort Ternan fossil fauna. *Fossil Vertebrates of Africa* 2:243–323.
- . 1978. Bovidae. In *Evolution of African Mammals*, eds. V. J. Maglio and H. B. S. Cooke, 540–572. Cambridge: Harvard University Press.
- . 1980. Fossil Bovidae (Mammalia) from Langebaanweg, South Africa. *Annals of the South African Museum* 79(8):2134–337.
- . 1985. The Bovidae of the Omo Group deposits. In *Les faunes Plio-Pleistocènes de la basse vallée de l'Omo (Ethiopie)*, eds. Y. Coppens and F. C. Howell, 1:119–191. Paris: Cahiers de Paleontologie.
- . 1987. Fossil Bovidae from Laetoli. In *Laetoli: A Pliocene site in northern Tanzania*, eds. M. D. Leakey and J. M. Harris, 378–408. Oxford: Clarendon Press.
- . 1990. Evolution and dispersal of African Bovidae. In *Horns, pronghorns, and antlers*, eds. G. A. Bubenik and A. B. Bubenik, 195–227. New York: Springer-Verlag.
- Géze, R. 1980. Les Hippopotamidae (Mammalia, Artiodactyla) du Plio-Pleistocene de l'Ethiopie (Afrique orientale). Thèse, Université de Paris VI.
- . 1985. Répartition paléocécologique et relations phylogénétiques des Hippopotamidae (Mammalia, Artiodactyla) du néogène d'Afrique Orientale. In *L'environnement des hominidés au Plio-Pleistocène*, eds. Y. Coppens and M. Beden, 81–100. Paris: Fondation Singer-Polignac, Masson.
- Hamilton, W. R. 1973. The lower Miocene ruminants of Gebel Zelten, Libya. *Bulletin of the British Museum (Natural History)*, *Geology* 21:76–150.
- . 1978. Fossil giraffes from the Miocene of Africa and a revision of the phylogeny of the Giraffoidea. *Philosophical Transactions of the Royal Society, series B* 283:165–229.
- Harris, J. M. 1976a. Cranial and dental remains of *Deinotherium bozasi* (Mammalia, Proboscidea) from East Rudolf, Kenya. *Journal of Zoology* 178:57–75.
- . 1976b. Pliocene Giraffidae (Mammalia, Artiodactyla) from Cape Province. *Annals of the South African Museum* 69:325–353.
- . 1978. Deinotheriidae and Barytheriidae. In *Mammalian evolution in Africa*, eds. V. J. Maglio and H. B. S. Cooke, 315–332. Cambridge: Harvard University Press.
- . 1983a. Family Deinotheriidae. In *Koobi Fora Research Project, Vol. 2—The fossil ungulates: Probos-*

- cidae, *Perissodactyla*, and *Suidae*, ed. J. M. Harris, 22–39. Oxford: Clarendon Press.
- . 1983b. Family Suidae. In *Koobi Fora Research Project*, Vol. 2—*The fossil ungulates: Proboscidea, Perissodactyla, and Suidae*, ed. J. M. Harris, 215–302. Oxford: Clarendon Press.
- . 1991a. Family Hippopotamidae. In *Koobi Fora Research Project*, Vol. 3—*The fossil ungulates: Geology, fossil artiodactyls, and palaeoenvironments*, ed. J. M. Harris, 31–85. Oxford: Clarendon Press.
- . 1991b. Family Bovidae. In *Koobi Fora Research Project*, Vol. 3—*The fossil ungulates: Geology, fossil artiodactyls, and palaeoenvironments*, ed. J. M. Harris, 139–320. Oxford: Clarendon Press.
- . 2003a. Lothagam Giraffidae. In *Lothagam: The dawn of humanity in Africa*, eds. M. G. Leakey and J. M. Harris, 523–530. New York: Columbia University Press.
- . 2003b. Lothagam Bovidae. In *Lothagam: The dawn of humanity in Africa*, eds. M. G. Leakey and J. M. Harris, 531–579. New York: Columbia University Press.
- Harris, J. M., F. H. Brown, and M. G. Leakey. 1988. Stratigraphy and palaeontology of Pliocene and Pleistocene localities west of Lake Turkana, Kenya. *Contributions in Science* 399:1–128.
- Harris, J. M., and T. E. Cerling. 1998. Isotopic changes in the diet of giraffids. *Journal of Vertebrate Paleontology* 18(suppl.):49A.
- . 2002. Dietary adaptations of extant and Neogene African suids. *Journal of Zoology* 256:45–54.
- Harris, J. M., and M. G. Leakey. 2003a. Lothagam birds. In *Lothagam: The dawn of humanity in Africa*, eds. M. G. Leakey and J. M. Harris, 161–166. New York: Columbia University Press.
- . 2003b. Lothagam Rhinocerotidae. In *Lothagam: The dawn of humanity in eastern Africa*, eds. M. G. Leakey and J. M. Harris, 371–385. New York: Columbia University Press.
- . 2003c. Lothagam Suidae. In *Lothagam: The dawn of humanity in Africa*, eds. M. G. Leakey and J. M. Harris, 485–519. New York: Columbia University Press.
- Harris, J. M., and T. D. White. 1979. Evolution of the Plio–Pleistocene African Suidae. *Transactions of the American Philosophical Society* 69:1–128.
- Hendey, Q. B. 1981. Palaeoecology of the Late Tertiary fossil occurrences in “E” Quarry, Langebaanweg, South Africa, and a reinterpretation of their geological context. *Annals of the South African Museum* 84:104.
- Hooijer, D. A. 1972. A late Pliocene rhinoceros from Langebaanweg, Cape Province. *Annals of the South African Museum* 29(9):151–191.
- Hooijer, D. A., and V. J. Maglio. 1974. Hipparions from the late Miocene and Pliocene of northwestern Kenya. *Zoologische Verhandlungen Leiden* 134:3–34.
- Hooijer, D. A., and B. Patterson. 1972. Rhinoceroses from the Pliocene of northwestern Kenya. *Bulletin of the Museum of Comparative Zoology* 144(1):1–26.
- Hopwood, A. T. 1936. New and little-known fossil mammals from the Pliocene of Kenya Colony and Tanganyika Territory. *Annals and Magazine of Natural History* series 10, 17:636–638.
- Janis, C. M., and K. M. Scott. 1987. The inter-relationships of higher ruminant families with special emphasis on the Cervidae. *American Museum Novitates* 2893:1–85.
- Joleaud, L. 1920. Sur la présence d’un Gavialide du genre *Tomistoma* dans le Pliocène d’eau douce de l’Ethiopie. *Comptes Rendus de l’Académie des Sciences, Paris* 70:816–818.
- Kingdon, J. 1974. *East African mammals*, Vol. IIB. Hares and rodents. Chicago: University of Chicago Press. 704 pp.
- . 1982. *East African mammals*, Vol. 3 (part C). Bovids. London: Academic Press.
- . 1958. Some East African Fossil Suidae. *Fossil Mammals of Africa* 14:1–133.
- Leakey, M. G. 1982. Extinct large colobines from the Plio–Pleistocene of Africa. *American Journal of Physical Anthropology* 58:153–172.
- Leakey, L. S. B. 1965. *Olduvai Gorge 1951–1961: Fauna and background*. Cambridge: Cambridge University Press.
- . 1987. Colobinae (Mammalia, Primates) from the Omo Valley, Ethiopia. In *Les faunas Plio–Pleistocènes de la Basse Vallée de l’Omo (Ethiopie)*, Tome 3, *Cercopithecidae de la Formation Shungura*, 148–169. Cahiers de Paleontologie, Travaux de Paleontologie Est-Africaine, Paris: Editions du CNRS.
- . 1993. Evolution of *Theropithecus* in the Turkana Basin. In *Theropithecus: The rise and fall of a primate genus*, ed. N. G. Jablonski, 85–123. Cambridge: Cambridge University Press.
- Leakey, M. G., and E. Delson. 1987. Fossil Cercopithecidae from the Laetoli Beds, Tanzania. In *Laetoli: A Pliocene site of northern Tanzania*, eds. M. D. Leakey and J. M. Harris, 91–107. New York: Oxford University Press.
- Leakey, M. G., C. S. Feibel, I. McDougall, and A. Walker. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature* 376:565–571.
- Leakey, M. G., C. S. Feibel, I. McDougall, C. Ward, and A. Walker. 1998. New specimens and confirmation of an early age for *Australopithecus anamensis*. *Nature* 393:62–66.
- Leakey, M. G., and J. M. Harris. 2003. Lothagam: Its significance and contributions. In *Lothagam: The dawn of humanity in east Africa*, eds. M. G. Leakey and J. M. Harris, 625–660. New York: Columbia University Press.
- Leakey, M. G., M. F. Teaford, and C. V. Ward. 2003. Cercopithecidae from Lothagam. In *Lothagam: The dawn of humanity in East Africa*, eds. M. G. Leakey and J. M. Harris, 201–248. New York: Columbia University Press.
- MacInnes, D. G. 1942. Miocene and post-Miocene Proboscidea from East Africa. *Transactions of the Zoological Society of London* 25:33–106.
- Maglio, V. J. 1970. Four new species of Elephantidae from the Plio–Pleistocene of northwestern Kenya. *Breviora* 341:1–43.
- . 1973. Origin and evolution of the Elephantidae. *Transactions of the American Philosophical Society* 63(3):149 pp.
- Meylan, P. A., and W. Auffenberg. 1986. New land tortoises (Testudines: Testudinidae) from the Miocene of Africa. *Zoological Journal of the Linnean Society* 86:279–307.
- Meylan, P. A., B. S. Weig, and R. C. Wood. 1990. Fossil soft-shelled turtles (Family Trionychidae) of the Lake Turkana basin, Africa. *Copeia* 1990(2):508–528.
- Partridge, T. C., D. E. Granger, M. W. Caffee, and R. J.

- Clarke. 2003. Lower Pliocene hominid remains from Sterkfontein. *Science* 300:607–612.
- Patterson, B. 1968. The extinct baboon, *Parapapio jonesi*, in the early Pleistocene of northwestern Kenya. *Breviora* 282:1–4.
- Patterson, B., A. K. Behrensmeyer, and W. D. Sill. 1970. Geology of a new Pliocene locality in northwestern Kenya. *Nature* 256:279–284.
- Petrocchi, C. 1954. I proboscidi di Sahabi. *Rendiconti dell'Accademia Nazionale dei XL* 4(1953–1954):1–66.
- Pickford, M. 1983. On the origins of Hippopotamidae together with descriptions of two new species, a new genus and a new sub-family from the Miocene of Kenya. *Geobios* 16:193–217.
- Powers, D. W. 1980. Geology of Mio–Pliocene sediments of the lower Kerio River Valley. Ph.D. dissertation, Princeton University. 182 pp.
- Reed, K. A. 1997. Early hominid evolution and ecological change through the African Plio–Pleistocene. *Journal of Human Evolution* 32:289–322.
- Sauer, E. G. F. 1972. Ratite eggshells and phylogenetic questions. *Bonner Zoologische Beiträge* 23:3–48.
- Storrs, G. W. 2003. Late Miocene–Early Pliocene crocodilian fauna of Lothagam, southwest Turkana Basin, Kenya. In *Lothagam: The dawn of humanity in eastern Africa*, eds. M. G. Leakey and J. M. Harris, 137–159. New York: Columbia University Press.
- Tassy, P. 2003. Elephantoida from Lothagam. In *Lothagam: The dawn of humanity in eastern Africa*, eds. M. G. Leakey and J. M. Harris, 331–358. New York: Columbia University Press.
- Tchernov, E. 1976. Crocodylidae from the Pliocene/Pleistocene formations of the Rudolf Basin. In *Earliest man and environments in the Lake Rudolf Basin*, eds. Y. Coppens, F. C. Howell, G. Isaac, and R. E. F. Leakey, 370–378. Chicago: University of Chicago Press.
- . 1986. Evolution of the crocodiles in East and North Africa. *Cahiers de Paléontologie*. Paris: Centre National de la Recherche Scientifique.
- Thomas, H. 1979. Les Bovidés du Miocène supérieur des couches de Mpesida et de la formation de Lukeino (District de Baringo, Kenya). *Proceedings of the 8th Pan-African Congress of Prehistory and Quaternary Studies*, Nairobi, 1977, 82–91.
- van der Made, J. 1999. Biometrical trends in the Tetraconodontinae, a subfamily of pigs. *Transactions of the Royal Society of Edinburgh: Earth Sciences* 89: 199–225.
- Vrba, E. S. 1984. Evolutionary pattern and process in the sister group Alcelaphini–Aepycerotini. In *Living fossils*, eds. H. Eldredge and S. M. Stanley, 62–79. New York: Springer-Verlag.
- . 1985. African Bovidae: Evolutionary events since the Miocene. *South African Journal of Science* 81: 263–266.
- . 1987. New species and a new genus of Hippotragini (Bovidae) from Makapansgat Limeworks. *Palaeontologia Africana* 26(5):47–58.
- . 1995. The fossil record of African antelopes (Mammalia, Bovidae) in relation to human evolution and climate. In *Paleoclimate and evolution with emphasis on human origins*, eds. E. S. Vrba, G. H. Denton, T. C. Partridge, and L. H. Burkle, 385–424. New Haven: Yale University Press.
- . 1997. New fossils of Alcelaphini and Caprinae (Bovidae, Mammalia) from Awash, Ethiopia, and phylogenetic analysis of Alcelaphini. *Palaeontologia Africana* 34:127–198.
- Ward, C. V., M. G. Leakey, and A. C. Walker. 1999. The new hominid species *Australopithecus anamensis*. *Evolutionary Anthropology* 7:197–205.
- . 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *Journal of Human Evolution* 4:255–368.
- Wesselman, H. B. 1984. The Omo micromammals: Systematics and paleoecology of early man sites from Ethiopia. *Contributions in Vertebrate Evolution* 7: 1–219.
- Weston, E. M. 1997. A biometrical analysis of evolutionary change within the Hippopotamidae. Ph.D. dissertation, University of Cambridge.
- . 2003. Fossil Hippopotamidae from Lothagam. In *Lothagam: The dawn of humanity in eastern Africa*, eds. M. G. Leakey and J. M. Harris, 441–483. New York: Columbia University Press.
- Winkler, A. J. 1998. New small mammal discoveries from the early Pliocene at Kanapoi, West Turkana, Kenya. *Journal of Vertebrate Paleontology* 18(suppl.):3:87A.
- WoldeGabriel, G., T. D. White, G. Suwa, P. Renne, J. de Heinzelin, W. K. Hart, and G. Heiken. 1994. Ecological and temporal placement of Early Pliocene hominids at Aramis, Ethiopia. *Nature* 371:330–333.
- Wood, R. C. 1983. *Kenymys williamsi*, a fossil pelomedusid turtle from the Pliocene of Kenya. In *Advances in herpetology and evolutionary biology: Essays in honor of Ernest E. Williams*, eds. A. J. G. Rhodin and K. Miyata, 74–85. Cambridge, Massachusetts: Museum of Comparative Zoology, Harvard University.
- . 2003. Fossil turtles from Lothagam. In *Lothagam: The dawn of humanity in eastern Africa*, eds. M. G. Leakey and J. M. Harris, 115–136. New York: Columbia University Press.
- Wynn, J. G. 2000. Paleosols, stable carbon isotopes, and paleoenvironmental interpretation of Kanapoi, northern Kenya. *Journal of Human Evolution* 39: 411–432.

APPENDIX

PRELIMINARY ASSESSMENT OF THE KANAPOI MICROMAMMALS

ALISA J. WINKLER

Order Chiroptera

Family Hipposideridae

Hipposideros Gray, 1831

Hipposideros spp.

Winkler (1998) reported a large and small species of *Hipposideros* (Old World leaf-nosed bats), represented mainly

by postcrania and isolated teeth, from the “Bat Site” locality (WT 3409). In Africa, *Hipposideros* is currently known from seven superspecies or species groups (Kingdon, 1974). *Hipposideros* may roost in a variety of shelters, including caves, holes in the ground, hollow trees, and in undergrowth. Several species are known to roost with other species of bats. The size of roosting aggregations varies from several to over 1,000 individuals. At the “Bat Site” locality, the large concentration of bats, relative

scarcity of other taxa, and little evidence of alteration or transport of the bones and teeth suggest that this assemblage represents an attritional accumulation under a roost site.

Order Insectivora

Family Soricidae

Subfamily Crocidurinae

Crocidurinae gen. and sp. indet.

Two incomplete mandibles of shrews are currently known from Kanapoi. At least one of these may be referable to *Myosorex* Gray, 1838. This genus is known from Africa at present and is also reported from the African Plio-Pleistocene (Hendey, 1981; Wesselman, 1984).

Order Macroscelidea

Family Macroscelididae

Elephantulus Thomas and Schwann, 1906

Elephantulus sp.

Three specimens of *Elephantulus* have been recovered so far from Nzube's Mandible Site (WT 3227). Kanapoi includes one of the earliest known records of the genus, the other being Langebaanweg (Hendey, 1981). The present range of *E. rufescens* (Peters, 1878) (spectacled or long-eared elephant shrew) includes thickets in South Turkana (Coe, 1972).

Order Lagomorpha

Family Leporidae

Leporidae gen. and sp. indet.

Dental and postcranial remains of lagomorphs are known from Nzube's Mandible Site and several other sublocalities at Kanapoi. Lagomorphs are well represented in modern and fossil African faunas.

Order Rodentia

Winkler (1998) reported a rich microvertebrate fauna associated primarily with the locality that yielded the holotype mandible of *Australopithecus anamensis* (Nzube's Mandible Site). Recovered materials included cranial and postcranial remains of fish, amphibians, reptiles, birds, and mammals. The microvertebrates from Nzube's Mandible Site likely represented a concentration of owl pellets, with some attritionally incorporated taxa. The mammalian specimens were dominated by a small species of the gerbil *Tatera* Lataste, 1882, and by murine rodents. There is also a new species of ground squirrel (*Xerus*) Hemprich and Ehrenberg, 1832, and a new dendromurine genus that appears to be the sister taxon to *Steatomys* Peters, 1846, (fat mice). Although the Kanapoi rodents have yet to be studied in detail, the fauna appears most similar to that from the lower Shungura Formation of the lower Omo Valley (Wesselman, 1984). At the generic level, the Kanapoi rodents are strikingly similar to those present today in the South Turkana region (Coe, 1972). Based on a comparison with modern analogues, the Kanapoi small mammals suggested a relatively dry climate and open habitat.

Received 26 December 2002; accepted 23 May 2003.